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AN ANALYSIS OF INTROGRESSION IN A POPULATION OF STEMLESS WHITE VIOLETS*

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Speciation in the stemless white violets has generally been recognized as complicated. There are numerous taxa; variability from plant to plant in any one population is frequently high; and differences from one population to another are sometimes of uncertain interpretation. Careful field and herbarium work (Fernald, 1950, and Russell, 1953) has cleared up some of the complexities but considered in the large has raised as many problems as it has solved.

On two occasions I have had the opportunity to make brief but intensive studies of local populations, once in Minnesota with Dr. Norman Russell, once in Pelham, Massachusetts, with Dr. R. P. Levine and the biology majors from Amherst College. On the latter trip, two days were spent examining variable local populations of *Viola pallens* in the Pelham Hills. They were studied in the field; a critical mass collection was made; the variation patterns were analyzed in the laboratory, first morphologically, and then by simple statistical and semigraphical devices. From the data, introgression with a second taxon was established and a detailed technical description of it was drawn up by the method of extrapolated correlates. A second field trip confirmed the presence of just such a violet in the same area (the Pelham Hills), but since it was just barely coming into flower further studies of it were not possible. Neither species grows in the neighborhood of St. Louis, nor could readily be grown there because of climatic and soil differences. No further work with the problem is planned, but the data and the analyses are being put on record since they illustrate certain phenomena of introgressive variability which are of general importance. I am indebted to Dr. Levine for the opportunity of making this analysis and to a score of his colleagues and students for technical assistance.

After the mass collection was brought back to the laboratory, flowers from each plant were placed in numbered culture dishes to prevent withering, and special features of the variation pattern were assigned to groups of two to four students, first for morphological analysis and then for measurement. As soon as the measure-

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ments were completed, frequency distributions of each variable and scatter diagrams indicating the relationships between variables were prepared. One pair of students assisted in coordinating the work of the entire laboratory, seeing that each group studied each plant and that the measurements and grades were added to the master list. In this way the equivalent of several days of technical work was completed in one afternoon.

Vegetative propagation is well developed in *Viola pallens*. Nearly all the plants examined bore several flowers and a few of them made large mats with numerous blooms. This was taken advantage of in two ways: (1) Examination of the variation within and between plants made it possible to choose characters which were relatively independent of environmental effects. (2) In selecting flowers for measurement, great care was taken to choose a specimen which was typical of the plant on which it was borne. This minimized the effects of insect attack and other injuries.

It was soon apparent that the most conspicuous plant-to-plant variable in the population of *Viola pallens* was the amount of color on the lower petals. Repeated experience with such problems in various genera of plants and animals has demonstrated that by persistence and biological acumen a vague difference of this sort can nearly always be broken down into numerous more-primary variables each of which can then be dealt with quite precisely. Various means were tried out for recording and measuring the plant-to-plant differences in colored veins in terms of such primary features as number and position of veins, branching of veins, width of veins, deposition of color between the veins, and the like. In the time available it was possible to resolve the variation in color into the primary variables shown in fig. 1.

Other obvious variables in the population were leaf shape, leaf color, leaf pubescence, and the clubbed hairs towards the base of certain petals. It was not possible to find an effective way of measuring the latter variable. The hairs were varying in size, in the closeness of their spacing, and in the pattern of their distribution on the petals. In some flowers they tended to be in regular lines, in others not. Sometimes they were more dense in certain areas, sometimes not. There were obviously several different variables at work here, but in the time available it was not possible to pin them down. One of the basic difficulties was that *Viola pallens* is typically without any such hairs on the wing petals, and there is therefore no direct method by which we can determine its basic hair pattern (a very different thing from hair presence). This illustrates a major point to be kept in mind in the analysis of introgressive variability. Glabrous species, when hybridizing with pubescent species, nearly always bring in strong hair patterns of their own which of course are invisible in the species in which they originated. Similarly, white-flowered species when hybridizing with species whose flowers are colored nearly always bring in color modifiers and color patterns which were invisible or virtually so in the species whence they came. White-flowered species, for instance, are frequently genetically blue, though they may show no color or only a few lines or flushes of dark blue. If such a species is crossed to one with bright magenta-pink

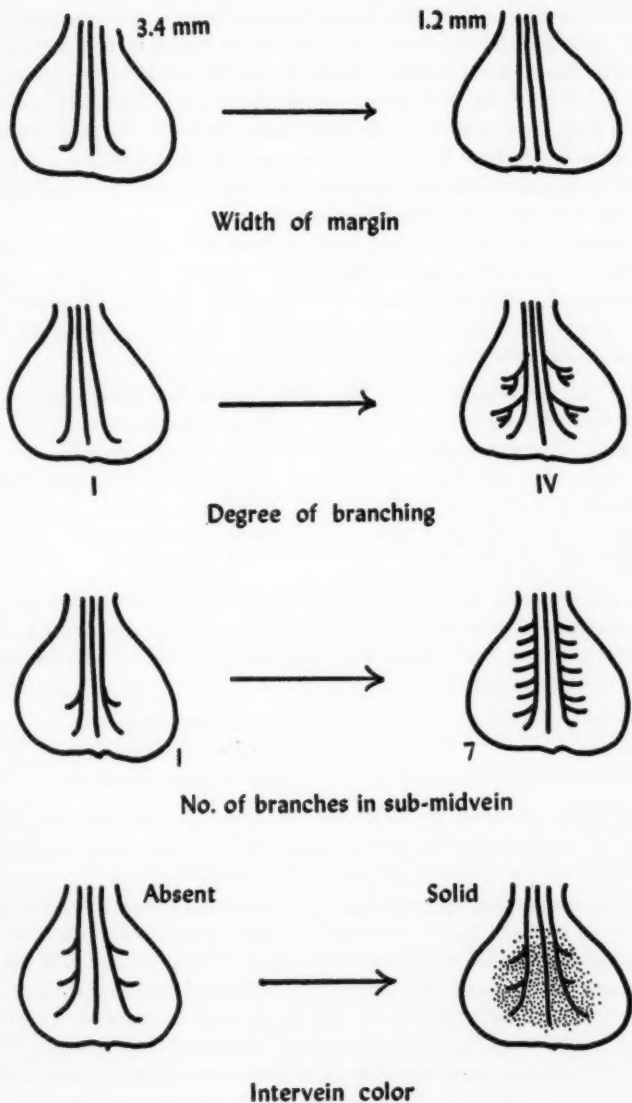


Fig. 1. The four variables which were responsible for the variation in color in the spur petals. The extremes within the population are shown somewhat diagrammatically. The spur petals are shown as if they were always the same size and shape; actually they varied a great deal for these characters.

flowers, and this hybrid back-crossed to the white, the resulting three-quarter bloods will show blue or light blue in many of the flowers. This statement is based primarily upon genetic data from the breeding of *Brachyceras* water-lilies, from introgressive experimental evidence from *Oxytropis albiflora* and *O. Lambertii* (Anderson, 1953), from hybridization between *Aquilegia flabellata* and *A. canadensis*, and from observations on wild and garden hybrids in the genus *Pblox*.

Leaf shape would have been easier to analyze had the leaves been fully mature. Color and pubescence could have been scored in the leaves but as a matter of convenience were scored in the peduncle of the flowers.

After these several variables had been analyzed and measured it was simple to demonstrate by means of a pictorialized scatter diagram that they were organized in two complexes. The more closely it was possible to follow all seven of them, the easier it was to demonstrate that these six *on the average* tended to associate themselves in the following combinations:

Wide margined petals	Narrow margined petals
Few colored veins	Many colored veins
Colored veins unbranched	Colored veins branched
No color between veins	Highly colored between veins
Glabrous pedicels	Pubescent pedicels
Little or no anthocyanin in epidermis of peduncle	Much anthocyanin in epidermis of peduncle

When the specimens had been graded in terms of all seven variables it was possible by comparing the two extreme classes (i.e., those which were low for all seven of these characters vs. those which were high for all seven) to add the following characters to these complexes:

Very early flowering	Later flowering
Delicate	Coarser throughout
Highly fragrant	Little or no fragrance

Extrapolating character by character we drew up the following technical description of the hypothetical species which could account (by hybridizing and back-crossing) for the variation pattern in this population:

A later-flowering, less fragrant, slightly coarser species than *V. pallens*; peduncles pubescent, strongly tinged with anthocyanin; flower white, the lower three petals conspicuously veined with purple and with a blue-purple blotch in the center of the keel petal; wing petals most probably with clubbed hairs near the base. Much of this description would apply equally well to either *Viola blanda* or *V. incognita*, two similar (and frequently confused) species of eastern North America. On the second field trip violets answering this description were found in close proximity to those previously collected. They were so much later in their flowering season that the details of their color pattern could not yet be precisely determined.

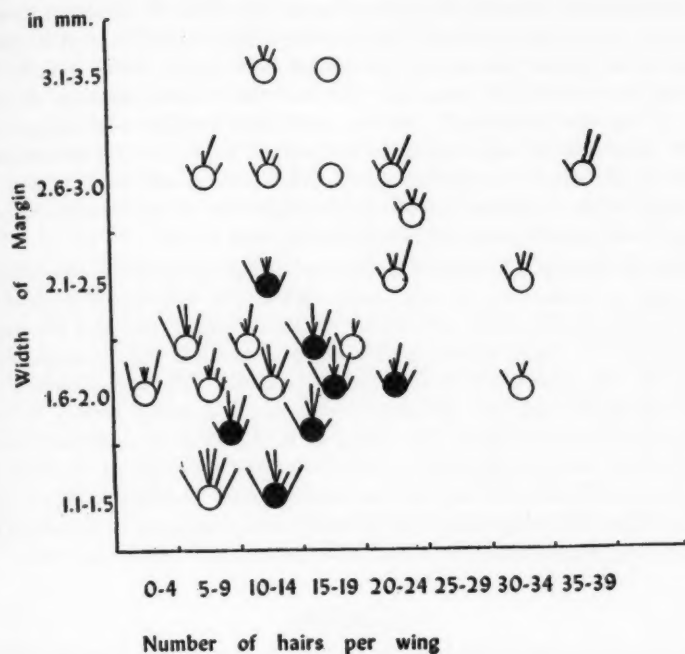


Fig. 2. Pictorialized scatter diagram showing the variation for seven characters in the population studies. Each circle represents a single individual. Black circles denote a flower with a heavy blotch on the spur petal.

Two of the characters are indicated along the margins. It will be noted that the number of hairs shows no very definite association with any of the other characters.

Five characters are indicated by rays:—

The rays departing from the equator of each dot designate the number of branches in the submedian veins: no equatorial ray, 1 branch; 1 short ray to the left, 2-3 branches; 2 short rays, 4 branches; 1 long and 1 short ray, 5 branches; 2 long rays, 6-7 branches.

Number of wing-petal veins shown by the apical ray which slants to the left: no ray, 0-3 veins; short ray, 4-7 veins; long ray, 8-10 veins.

Hairs on pedicel shown by erect apical ray: no ray, 1-4 hairs; short ray, 5-9 hairs; long ray, 10-13 hairs.

Degree of branching shown by apical ray slanting to the right: no ray, branching of first degree only; short ray, branching of second degree; long ray, branching of third or fourth degree.

Position of pedicel hairs shown by shoulder ray slanting to right (at the right between the apical and equatorial rays): no ray, no hairs or hairs very faint; short ray, hairs extending up to crook of pedicel; long ray, hairs extending from part way up to the crook of the entire pedicel.

From the data presented here, the introgression responsible for the variation in this population of *V. pallens* might have come from either *V. blanda* or from *V. incognita*. The presence of clubbed hairs on the wing petals of many of the plants, as well as the general distribution patterns of both species, would indicate that *V. incognita* was certainly involved. The fact that clubbed hairs on the wing petals did not seem to be closely associated with either complex would suggest that both *V. blanda* and *V. incognita* might be involved, were it not for the difficulties in assaying hair pattern in glabrous species which have already been discussed. A field study similar to this one carried on a fortnight later in the spring in the same locality would probably yield critical evidence on these points.

After the differences between *V. pallens* and its introgressants had been analyzed it was easy to demonstrate the relationship between the micro-distribution of the introgressants and the ecology of the site. The road wound through a hilly region of second-growth forests which were beginning to resemble well-established mixed hardwoods with silver birch, hemlock, maple, and ash. The actual roadway and its drainage ditches had been repeatedly relocated, and extensive grading had been carried on within a few years. The plants of *V. pallens* in the woodlands showed a minimum of introgression whereas collections from the ridges of excavated soil along the roadside showed a maximum of branched veins, blotched petals, etc. This increased degree of introgression in disturbed sites has frequently been reported and its general significance made the subject of a special study (Anderson, 1948).

CONCLUSION

Increasing experience with species hybrids in the field and the experimental plot has shown that what looks like a simple difference between two species can often be broken down into a number of more primary ones, each of which is itself apparently multifactorial. In this example the difference between a heavily marked spur petal and a lightly marked one can be demonstrated as resulting from the following more basic differences:

- Number of colored veins
- Branching of veins
- Restriction or non-restriction of colored veins to center of petal.
- Interveinal blotching.

In *Adenostoma* (Anderson, 1952, 1954) dense versus open panicles can be demonstrated as resulting from the following more basic differences, each of which behaves as if it were multifactorial and is only loosely associated with any one of the others:

- Long vs. short internodes
- Non-telescoped vs. telescoped internodes
- No evident tertiary branches vs. many evident tertiary branches
- One flower per node vs. several flowers per node.

The field analysis of such examples of introgression as that just described should enable us eventually to find our way to the most efficient techniques and best experimental materials for detailed genetic analysis of quantitative characters. This entire field of Genetics, as a truly experimental science, has scarcely advanced in effective techniques since East first established the multiple-factor hypothesis and set up a series of criteria for testing it. Modern work on the subject has been largely confined to expertly contrived mathematical models, indicating how quantitative characters might evolve. While very stimulating, these models are a long way from any really concrete evidence showing chromosome by chromosome and segment by segment how any particular character is inherited or, on the other hand, demonstrating with incontrovertible proof how any particular chromosome is organized in between the marker genes.

This paper is one of a series illustrating exact techniques for the morphological analysis of variable populations. These techniques are at last approaching the precision which will permit their use in decisive experiments on the genetics of quantitative inheritance. These studies have seemed to most observers as a means by which the exact methods of Genetics could be used to illuminate the problems of Taxonomy. They are now beginning to be revealed as an attempt to refine from the wider observational basis of Taxonomy, precise evidence for analyzing a basic problem in Genetics. Logical deduction, no matter how acute, cannot serve forever in the place of direct evidence on so fundamental a question.

SUMMARY

Field studies of a population of *Viola pallens* resolved the bulk of the variability into two complexes, one of which is *V. pallens* and the other a later, slightly coarser, and more deeply pigmented species. The purple petal spot of this latter complex is shown to result from the following more primary variables, each of which is apparently multi-genic:

Wide marginal area without veins	Narrow marginal area
Few colored veins	Many colored veins
Few branched veins	Many branched veins
No interveinal color	Heavy interveinal color

The bearing of such studies on the genetics of quantitative inheritance is specifically pointed out.

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"SOME PECULIARITIES OF MAIZE IN ASIA" BY N. N. KULESHOV

Translated by HAROLD J. KIDD and HOWARD C. REYNOLDS

Illustrations re-drawn from the published photographs by Ellen Kern Lissant

TRANSLATORS' NOTE: The following is a translation from the Russian of a paper by N. N. Kuleshov (Bull. Appl. Bot., Genet., and Pl. Breed. 19:325-374. 1928. English summary, pp. 370-374). It is of particular interest in view of recent findings concerning the geography of races of maize. The only extensive studies of maize in the Orient are here described by the author. Kuleshov's entire work has been translated and included with the exception of his literature review of the American studies of waxy maize.

The English used in this translation will strike a number of people as being quite repetitive and wordy. For instance, the word *obraztsy*, which we have translated *collections*, appeared again and again. This characteristic, along with the redundant phrases and wordiness, has been retained wherever the meaning was sufficiently clear. We have attempted to retain in English something of the quality of the Russian original.

Regarding the references missing from the *Literature Cited*, we should mention in fairness to Dr. Kuleshov that there are innumerable evidences of careless editing.

In the work of the American investigators, G. N. Collins and J. H. Kempton, one meets an array of very interesting characters and attributes which are unknown in maize from the American continent but which were discovered in collections of maize from Asia.

During the years 1926 and 1927, relatively vast amounts of material [data] concerning the maize of Asia passed through the All-Union Institute of Applied Botany, being composed of both laboratory and field studies. From this material it was possible to expand the observations of Collins and Kempton and to establish an array of new peculiarities in the maizes of Asia which are unknown to the American investigators.

Since we are planning a future publication of the complete work on Asian maize, in the present preliminary communication we will briefly bring out only the most interesting of the facts which have been established.

All the material which has been studied up to the present time is listed in the following table, and consists of collections from different regions of Asia and Transcaucasia:

1. Asia Minor	65 collections
2. Persia	10 collections
3. Afghanistan	24 collections
4. Turkestan	65 collections
5. The Primorskii [Maritime] Province	85 collections
6. Manchuria	51 collections
7. Western China	18 collections
8. Japan	5 collections
9. India, Ceylon, Java	6 collections
10. Armenia	59 collections
11. Azerbaijan	10 collections

We will first pause to refer to the American work, passing thereafter to the data of our investigations.

I. THE DATA OF THE AMERICANS CONCERNING THE MAIZE OF ASIA [Omitted]

II. OUR OWN INVESTIGATIONS ON THE MAIZE OF ASIA

1. WAXY MAIZE

In the collection of maize which is located at the All-Union Institute of Applied Botany and New Crops, the presence of the type *waxy* was established in several cases.

(1) Of two collections received from the expedition of V. V. Markovich to Shanghai, one collection (on the cob) was white with a single blue kernel. The other (shelled corn) was called "Buo Rew" and contained a mixture of flinty, tooth-like yellow kernels along with an admixture of a single grain of the waxy type which had a light yellow color. Both collections were received in 1927.

(2) Four collections were received by the Institute from the experiment Station "Eho" in northern Manchuria, and in all four the waxy kernels have a yellow color of varying intensity. For two collections, the source was not designated, but for two it is known: Maize no. 136 "Nyan-pao-mi" ("sticky") from Ninguta, and maize no. 137 "Nyan-pao-mi" from Tubin. Both of these localities are in northern Manchuria.

(3) Two collections were received from the Primorskii Experiment Station. Their source was the village of Lukyanovka in the Utkin district, the Spassk territory of the Primorskii [Maritime] Province. One collection, no. 59, consists only of waxy maize of a light yellow color, which indicates that this sort has been cultivated here for more than twenty years. The second collection, no. 57, is principally flinty, but as an admixture it has a single kernel of the waxy type.

A comparison of all the collections listed above with the original collection received from Collins confirmed their undoubted classification as the waxy type.

We pause to consider the meaning of these findings. The collections from the region of Shanghai, received from V. V. Markovich, confirm once more the fact, which is known from the American literature, that waxy maize was discovered



Fig. 1. Plant of waxy maize, from Collins (1909).

and cultivated in this region. The collections from Ninguta and Tubin, which were sent by the Eho Station, establish a new place of discovery of waxy maize, which is significantly different from those three regions (Shanghai, Burma, and the Philippines) in which this maize was previously known.

In the seed catalogue of the Eho Experiment Station, these collections are filed under the name "Flint Corn, that is, flinty maize", but are labelled with the Russian name "Kleikaya" (sticky), and also the Chinese name "Nien-pao-mih". This Chinese name is differentiated from the other Chinese names "Pai-pao-mih", "Hei-pao-mih", and "Huang-pao-mih". There are, in the catalogue of the Eho Station, other cultures of flinty maize which force the supposition that the local populace differentiates this sort of maize from the ordinary flinty maize¹

The collections from the village of Lukyanovka, which is located approximately 300 kilometers east of Ninguta in the direction of Vladivostok, may be assumed to have a common origin with the waxy maize which is cultivated in Ninguta. None-the-less, on the basis of their being found here, we have sufficient grounds to assume that the growing of maize of the waxy type in this northern region of eastern Asia is wide-spread and is not especially rare.

If we now compare our apparently new discovery of waxy maize with what was previously known concerning its cultivation, we obtain the following: the Philippine Islands² are located at 5–15° north latitude; the upper Burma regions, 23–26° n. lat.; the Shanghai region, 31–32° n. lat.; the village of Lukyanovka, 43° n. lat.; Ninguta, 45° n. lat. Thus, at the present time, the area of diffusion of waxy maize has extended great distances from north to south, having been discovered in 1908 at Shanghai, again in 1915 in upper Burma, and 1920 in the Philippines. With our discovery [known] waxy maize immediately moves far to the north. This finding permits us to hypothesize about the limits of diffusion of this type in eastern Asia, but the incompleteness of maize investigations in this territory does not permit us to speak with certainty.

The matter of the extent of the limits of cultivation of waxy maize westward is of great interest. We have, unfortunately, insufficient material with which to trace the spread completely and clearly. At any rate, our material permits us to say with certainty that there is no waxy maize in central Asia or in Asia Minor. Turkestan was covered by us completely and in detail, from the China border to the Caspian Sea. Afghanistan was thoroughly explored by N. I. Vavilov, while P. M. Zhuzovskii travelled for two years in Asia Minor, and in neither place was waxy maize discovered. In 1927 we received eighteen collections of maize which were collected in western China from our consul in Kashgar, in none of which was there waxy maize. We have not yet spoken of the collections from the Caucasus and European areas. Here, of course, *waxy* does not occur.

¹The list of available seed at the Eho Station for exchange with other experiment stations. K. V. Zh. D., Harbin, 1926.

²These localities are those mentioned in the omitted review of American literature.



Fig. 2. Typical brachytic maize (from Kempton, 1921).



Fig. 3. The most widespread types of maize plants from Manchuria and western China, grown in Kharkov, 1927. Plants like Nos. 2 and 3 are more frequent in Manchuria.

In 1926 and 1927 we were fortunate enough to receive exceptionally interesting material from America. The expedition of S. M. Bukasov, of U. N. Voronov, and of S. V. Usepchuk brought us specimens of maize from Mexico, Guatemala, Panama, the island of Cuba, Venezuela, Colombia, Peru, and Bolivia. Approximately 2,000 collections were sent in all, representing a remarkably unusual variety of types. And here, in the principal center of variation from which maize originated, we, repeating the experiment of Collins,³ did not find maize of the type *waxy*. Thus, this particular type of maize is, apparently, peculiar to eastern Asia.

Since we already had in our collections samples of waxy maize, we planted them in 1927 and observed differences in their vegetative character. The majority of plants in collections from Shanghai had the attributes which were described by Collins: stiff leaf blades, silking ears hidden by the leaf sheaths, and the upper leaves displaced to one side and covering the panicle. The collections from Ninguta and Tubin were very singular in aspect, being thin-stalked plants with absolutely no tendency to produce lateral shoots. It is possible, however, that the conditions

³ Apparently the testing of kernels for the presence of waxy endosperm.

in Kharkov in 1927 contributed greatly to this situation, causing a small number of leaves and well-exserted panicles to be produced. This aspect was not peculiar to these collections only; similar plants predominated in all of the numerous Manchurian collections of flinty maize. Figure 3 depicts plants which are characteristic of the collections from Manchuria. For the most part, one encounters plants II and III, plant I being particularly rare.

A collection of waxy maize from the Primorskii Province was very extraordinary in its vegetative appearance and the make-up of its plants. All individuals were predominantly of the Manchurian type but among them were many plants similar to those we have termed the "European type". The latter is distinguished by stalks of average vigor which produce one to two lateral stalks similar in degree of development to their main stalk under favorable conditions, as is characteristic of the European flints. In individual plants one could observe attributes described by Collins for Shanghai maize: asymmetrical upper leaves which are straight and which cover the silking ears in their axils at the time pollen is shed (fig. 4).

TABLE II*
PHENOLOGICAL OBSERVATIONS ON SAMPLES OF WAXY MAIZE

	Date seeded	Date of shoot emergence	Date of pollination	Date of silking	Date of ripening	Plant height	Number of leaves
Shanghai from Markovich	5/12	5/28	8/25	8/27	-----	-----	20.7
Ninguta	5/12	5/28	7/23	7/22	9/12	207	17
Primorskii Province	5/12	5/28	7/19	7/23	9/12	188	17

*Table I is not included, since it was reprinted from Kempton (1921) in the omitted part of this paper and was not referred to elsewhere.

The data from phenological observations and measurements are presented in table II, representing individuals of the waxy type cultivated by us in Kharkov. Unfortunately, we were unable to compare them with Collins' plants from Shanghai, due to the fact that the seed of the latter had become inviable since its receipt at the Institute in 1923. The data in this table demonstrate that the Shanghai collections of V. V. Markovich were very late under Kharkov conditions, commencing flowering on August 25, and failing to ripen before the first killing frost on October 15. The collections from Ninguta and the Primorskii Province were very similar to one another and should be classed as early in maturity. The Shanghai collection is distinguished also from the other two by its large number of leaves.

In the collections from Ninguta it is interesting to note that the silks appear before pollen is shed. The plant height of the collection from Ninguta also indicates its dwarfness.



Fig. 4. Diversity of plants of waxy maize from the Primorskii Province, grown in Kharkov, 1927.

The above remarks on the vegetative peculiarities of our collections of waxy maize indicate that only the Shanghai collection was similar to that described by Collins in his first paper (1909). The Primorskii collection was similar in vegetative characters to the collections of flinty maize of that region. The Primorskii collection reflects the influence of the Manchurian type, on one hand, and the European, on the other. The latter has a wide distribution in the Primorskii Province, to which it had been brought by the Ukrainian settlers. A mere trace of the Shanghai type is retained by these plants. This fact is merely given and causes no surprise, since from the work of Collins we know that the endosperm factor *waxy* in his investigations was not linked with the vegetative attributes of the plant. However, such being the case, that in northern Manchuria waxy maize steadily acquires the aspect peculiar to most of the maize in this region, this observation attests to the fact that here waxy maize is not a newcomer.

Due to a misunderstanding, waxy maize has not yet received a generally accepted scientific Latin name, and different authors vary in referring to it. Americans usually use the term *waxy* but sometimes use the term *Chinese*, while German authors use *wachsig* or *chinesische*, etc. Since waxy maize of the average group as distinguished by Sturtevant occupies a special place, we suggest the Latin name *Zea mays ceratina* Kuleshov (spec. nov.).

2. THE PERSIAN TYPE OF MAIZE

In 1926, a large number of collections of maize were brought to two points, Kharkov and Sukhum. Almost the entire world was represented and the number of collections which were planted at both these two points approached 1,500. On the basis of the enormous amount of vegetative diversity in the collection, the Persian plants were sharply differentiated by their short height and the general condensation of the plant structures, as were those collections from the regions of middle Asia and Transcaucasia which border Persia.

These collections were again grown in 1927, and the peculiarity of the above specimens was again sharply distinguished from the variety of the world-wide collection, in spite of the exceptionally favorable conditions during the growing season. The 1927 study of these collections demonstrates that, besides shortness, the plants possessed an array of other extremely interesting peculiarities. The peculiarity [probably shortness] was expressed by all collections from Persia which were studied, so we therefore termed this completely different appearance of maize plant the Persian type.

Let us now turn our attention to the characteristics of the collections in which the manifestations of the Persian type may be observed. Persia was represented in our seedlings by seven collections from Seistan and Zurabad, all of which were distinguished by the following characters: (1) shortness of the plants; (2) coarse, wide, and short leaves with stiff blades; (3) definite waviness of the leaf blades; (4) the poor exertion of the panicle which is covered by the stiff upper leaves; (5) the non-emergence of the silking ears at tasseling; (6) the correlation of the blooming of the male and female inflorescences, frequently developing protogyny. Figure 5 shows many of these characters very well. One may observe the shortness of the plants, the stiffness of the leaf blades and the waviness of their surfaces, the manner in which the stiff upper leaves cover the panicle, and the nearly-hidden silks of the plants in the leaf axils, illustrated under a higher magnification in fig. 6.

While closely related in the majority of these characters, several Persian collections were distinguished by their capacity to produce lateral shoots. Of seven collections grown in the field, five were characterized by an almost complete lack of the capacity to produce lateral shoots both years, whereas two collections expressed this capacity rather strongly. We must needs note, however, that the plants at the edges of the plots were observed to be surprisingly uniform in appearance. Figure 7 shows the vegetative appearance of the plants of the collections from Persia. The plant on the extreme right represents the striking bushiness of the Persian type plants.

The above photographs [illustrations] doubtless have shown the peculiarities of the plants which we have distinguished as the Persian type. However, for a more complete picture, we present several measurements of plants of the Persian type for comparison with measurements of the prevailing sorts, Minnesota 13 (*indentata*), and Longfellow (*indurata*), as well as the original *brachytic*, which was received by us through N. I. Vavilov from Emerson of North America. As



Fig. 5. Typical plant of Persian maize, grown in Sukhum, 1927.

indicated, the growing conditions during the seasons of 1926 and 1927 were very different, 1927 being much more favorable and producing more vigorous development of the plants. But since Minnesota 13 and Longfellow were sown both years, an opportunity for a comparison [of the plants in both seasons] still remains. *Brachytic* was sown only in 1927.

TABLE III
OBSERVATIONS ON MAIZE PLANTS IN 1926 AND 1927 (KHARKOV)

Name	Origin	Plant height		Number of leaves on main stem		Stem thickness		Number of stems		Panicle exertion		Number ears per plant	
		'26	'27	'26	'27	'26	'27	'26	'27	'26	'27	'26	'27
Persian 1701	Zurabad	94	104	16.3	1.5	1.0	1.0	0.4	2.0	1.0	2.0
Persian 1702	Zurabad	92	116	17.2	17.4	1.7	1.1	1.2	0.3	1.2	1.6	3.1
Persian 1698	Seistan	96	142	18.8	18.5	1.6	2.3	0.6	3.0	2.9	6.3
<i>Brachytic</i>	Emerson	118	24.0	2.4	1.0	1.0	1.0
Minne. 13	U. S.	147	211	15.4	16.0	1.7	1.0	1.4	5.8	7.5	1.0	1.4
Longfellow	U. S.	140	229	14.8	16.5	2.2	3.6	4.4	6.7	1.1	1.6

Let us view the data from the table (Table III). The shortness of the Persian type plants, in comparison with the other collections, is shown perfectly clearly. Collection no. 1701 was half as tall in 1927 as Minnesota 13 or Longfellow. It was even shorter than *brachytic*, having a height of 103 cm. as compared with 118 cm. for *brachytic*. In the number of leaves, the Persian collections exceeded Minnesota 13 and Longfellow, but were surpassed by *brachytic*, which produced 24 leaves.

As indicated above, a terminal brachyism produces a reduction of plant height by means of a shortening of the internodes, without reducing the number and length of other parts of the plants. It is interesting, in this connection, to compare the average length of internodes of the plants studied by us. Table IV presents the results of the appropriate computations on the data from Kharkov. The figures from this table tell us that the mean internode length in the Persian collections of maize show significant reduction in comparison with the common types. They do not approach the shortness observed in *brachytic* but in any case a deviation from the norm is indicated.

The thickness of the stems of the Persian collections is not only no less, but even somewhat greater than the taller farmer's varieties. All of these characters (shortness of plant, a large number of leaves, and thick stems), considered together, give the impression of a condensation of plant structure, approaching the appearance of *brachytic* in several respects.

TABLE IV
MEAN LENGTH OF INTERNODES IN MAIZE PLANTS, IN CENTIMETERS

	1926	1927
Persian 1701	-----	6.16
Persian 1702	5.35	6.55
Persian 1698	5.11	7.68
<i>Brachytic</i>	-----	4.92
Minnesota 13	9.55	13.2
Longfellow	9.46	13.8

The exertion of the panicle is perfectly clear from the figures in Table III. At the time during which the distance from the highest leaf to the lower panicle branches was calculated, in Minnesota 13 and Longfellow it was 6-7 cm.; in the Persian collections in 1927, it was 1-3 cm., but in 1926 it did not approach 1 cm., in several instances being even less than zero, that is, the panicle had not completely emerged from the sheath of the upper leaf. In *brachytic* the exertion of the panicle in 1927 was 1 cm.

Due to the small number of stems, the Persian collections nos. 1701 and 1702 present a characteristically non-bushy aspect, whereas no. 1698 is typified by a significant bushiness. The number of ears per plant of Persian maize is greater than in the types in common culture. In 1927 collection no. 1698 produced an average of 6.3 ears per plant.

Let us continue with a brief glance at the data of the phenological observations (Table V). In the length of the vegetative period the Persian collections present several types earlier than the farmers' varieties. But the essential peculiarity of their differentiation does not lie here. They are distinguished from the common types by their peculiar nature of flowering. As demonstrated in one of our previous

TABLE V
PHENOLOGICAL OBSERVATIONS IN 1927 AT KHARKOV

Collection	Date of seedling emergence	Date of pollination		Silking date		Ripening date
		10%	75%	10%	75%	
Persian 1701	5/27	7/27	8/3	7/25	8/2	9/20
Persian 1702	5/27	7/27	7/31	7/22	7/29	9/20
Persian 1698	5/27	7/27	7/31	7/23	7/31	9/20
Minne. 13	5/26	7/14	7/19	7/14	7/23	9/28
Longfellow	5/31	7/21	7/27	7/23	7/30	9/28



Fig. 6. Concealment of the silk in the axil and sheaf of the leaf in Persian maize, grown in Kharkov, 1927.

works, "the appearance of the silks lags approximately three days behind the shedding of pollen under conditions at Kharkov" (Kuleshova and Kuleshov, 1918). In contrast to what was published by us earlier as the usual order of flowering of maize under Kharkov conditions and to the observations on Minnesota 13 and Longfellow in 1927, the Persian collections began extruding silks several days earlier (2-5) than the onset of pollination, giving an especially clear protogynous character to the flowering instead of the protandry which is common for maize. This phenomenon must be met with very rarely in maize. In one of his papers Collins states that until 1912 he had not encountered a protogynous race of maize, and in 1912 practically all plants from two ears of "red pop corn" from Spain were protogynous (Collins, 1913). He also believes that the presence of a receptive stigma earlier than the onset of pollination aids self-pollination. We see a confirmation of that in the frequently striking uniformity of the plants of the Persian type, which remind one of the uniformity observed in "selfed strains".

Turkestan collections in the field present a fairly large diversity in vegetative type, but the average of this diversity is an array of collections which repeats the general picture of vegetative appearance which is given by the Persian collections. In fig. 8, the principal representative of the vegetatively diverse Turkestan maize is depicted. In nos. 4 and 5 we recognize the characteristic plants of the Persian type in the form of two of its variants—tillering and non-tillering.



Fig. 7. Vegetative diversity of maize plants in Persian collections grown in Kharkov, 1927. Collections Nos. 1701, 1702, and 1698 (from left to right) from Zurabad and Seistan.

The Persian type of plant was established for the following collections:

1. Collection no. 1449 from Mary (Merv).
2. Collections nos. 3434, 3435, 3436, 3437, and 3439 from the Shirabad region.
3. Collections nos. 3450, 3451, 3452, 3453, 3454, and 3455 from the Polotansk region.
4. Collection no. 3425 from Termez.
5. Collection no. 2783 from the Zerevshansk region.
6. Collections nos. 3388, 3389, 3390, 3391 from the Urta-Zerevshansk district.

Nos. 1449 and 3425 share the characteristics of representatives of the Persian type. In Table VI we present several data characterizing these collections. In general, the data from the table are nearly like those which we presented for the Persian collections, which are distinguished by an increased number of leaves and by a shorter vegetative period. These collections do not silk earlier than pollination, but, in some instances, the flowering of the male and female flowers was more closely correlated in 1927 than it was in the common types. An apparent expression of the Persian type was observed in numerous collections from upper Turkestan. Besides the above, we observed different features of the Persian type in a host of collections from the Tashkent region, being expressed now in the stiffness of the leaves, now in the exertion of the panicles, etc.

TABLE VI
OBSERVATIONS ON TURKESTAN COLLECTIONS IN 1926 AND 1927 AT KHARKOV

	1449 from Merv		3425 from Termez	
	1926	1927	1926	1927
Plant height	88	147	134
Number of leaves	21.0	20.1	19.5
Stem thickness	2.1	2.0
Panicle exertion	0.0	2.8	2.3*
Number of stems	3.3	3.3	1.2
Number of ears per plant	1.4	5.1	2.2
Date of seedling emergence	5/25	5/27
Date of pollination..... { 10%	7/30	8/6	8/4
{ 75%	8/8	8/12	8/9
Silking date..... { 10%	8/3	8/5	8/5
{ 75%	8/13	8/10	8/9
Ripening date**	10/2	10/2

* [Assumed. Original printing was "23".]

** Failed to ripen before frost.



Fig. 8. Vegetative diversity of maize plants in collections from Turkistan grown in Kharkov, 1927. Plants 4 and 5 are from collections 1449 and 3425 from Merv and Termez [respectively].



Fig. 9. Vegetative diversity of maize plants in collections from Armenia grown in Kharkov, 1927. Plant 4 is from collection 1632 from the Echmiadzin District.

In Armenia we also encountered a fairly large amount of vegetative diversity among the collections, the types of which are depicted in fig. 9. Plant no. 3 is distinguished among these plants by its short stature. In its basic features this plant is the same as the "bushy" Persian type, but with several deviations from the typical Persian plants. In the shorter plants of Armenia we observed only free-tillering types. Furthermore, their leaves were usually wider and longer than in the Persian type. In several collections they were significantly longer and had lost their stiffness. In Table VII we present data which are characteristic of the typical short plants from the Echmiadzin region in Armenia.

TABLE VII
OBSERVATIONS ON THE PLANTS IN COLLECTION 1632 FROM ARMENIA
GROWN AT KHARKOV

Year	Plant height	Number of leaves	Stem thickness	Number of stems	Panicle exertion	Ears per plant	Date of seedling emergence	Date of pollination		Silking date		Date ripe
								10%	75%	10%	75%	
1926	82	17.7	3.3	0.0	1.36	5/25	7/30	8/8	8/3	8/13*
1927	139	17.2	1.8	3.2	3.9	3.6	6/3	8/2	8/9	8/4	8/12	9/28

* Failed to ripen before frost.

Short plants which were almost exactly as described above were encountered in the following regions:

1. Collections 1625, 1636, and 1649 from the Erivan district.
2. Collections 1619, 1632, 1644, 1647, 1622, 1624, 1638, 1612, and 1705 from the Echmiadzin district.
3. Collections 1616 and 1709 from the Daralagez district.

Besides the collections which are enumerated above, we observed various indications of the Persian influence on collections which were derived from other regions.

TABLE VIII
OBSERVATIONS ON THE PLANTS OF SHORT HABIT FROM AZERBAIJAN,
GROWN AT KHARKOV, 1927

Collection	Plant height	Number of leaves	Stem thickness	Number of stems	Panicle exertion	Ears per plant	Seedling emergence	Date of pollination		Silking date		Ripening date
								10%	75%	10%	75%	
Apuheron 1782	140	20.1	2.7	1.0	2.3	1.5	5/29	7/24	7/31	7/24	7/31	9/20
Nakhichevan 1783	133	16.0	1.2	5.4	6.9	5/29	7/31	8/11*	8/2	8/13	10/2

* [Assumed. Originally printed "7/11".]



Fig. 10. Vegetative diversity of maize plants in collections from Azerbaijan, grown in Kharkov, 1927. Plants 4 and 5 are from collections 1783 and 1782 from Nakhichevan Rep. and the Apsheron Peninsula.

In Azerbaijan the presence of the non-tillering Persian type was established in collections from the Apsheron Peninsula. In the Nakhichevan region, which borders on Armenia, the variations of the Persian type as described for upper Armenia were seen (fig. 10).

Upon viewing the photograph more attentively, the zig-zag arrangement of the internodes of the plant on the extreme right may be observed. An instance of a similar zig-zag character was observed by Kempton in his studies of *brachytic*, which at once leads to a conjecture of a relationship between our short-stemmed and the well-known brachytic types. Data concerning the characteristics of the short plants which are represented in the photograph are given in Table VIII.

From the data presented, the aspect of the plants from Azerbaijan in comparison with what was stated concerning other regions is sufficiently clear. We wish to mention, however, that in the Apsheron collections we observed a remarkable correlation in male and female flowering time. The studies of the peculiarities of the maize plant which were investigated for the present paper and described under the name of the Persian type give a series of very interesting conclusions:

1. Maize plants short in height considering their normal number of leaves are represented in very widespread regions in central Asia and Transcaucasia.
2. The stiffness of the leaf blades also indicates that the Persian type is very widespread in these regions.

3. The degree to which the upper leaves cover the panicle is quite variable in its expression, indicating a rapid diffusion of the Persian type in the regions of central Asia and Transcaucasia as well as in eastern Asia. Fig. 11 represents the different types of this covering observed in Kharkov in 1927.

4. The concealment of the silking ears is no less widespread in these regions than the characters mentioned above.

We know (through an acquaintance with the work of the American workers) that Collins observed in collections of waxy maize from Shanghai: stiffness of the leaf blades, the panicle covered by the upper leaves, and the concealment of the silking ears. Our data demonstrate a wide distribution of these characters in Asia, as well as their correlation with a definite area. True, in our short plants of the Persian type we do not have that strong expression of brachyism observed by Kempton, but at any rate this shortness compared with normal plants or even with those having a somewhat greater number of leaves gives a basis for comparison with the expression of that character.

The study of the world-wide collection of maize which was conducted in 1926 and 1927 demonstrated that such precise expression of all the recapitulated characters and their delimitation to definite regions will not be observed anywhere else on earth: these extraordinary peculiarities are inherent only to the maize of Asia. The protogynous character of flowering, which is developed so clearly in the Persian collections of maize, is not so widespread in other regions of middle Asia and Transcaucasia. But, at any rate, the remarkable correlation of the timing of male and female flowering can be one of the very characteristic attributes of maize plants in central Asia.

We should still consider one morphological attribute which is frequently encountered in the maize of central Asia and Transcaucasia. This character is the shortening of the stem internodes. There are many exceptions among the described collections and the character may be met with in collections from different regions, but in central Asia it is more often seen than not. In conclusion, after all that has been related concerning the Persian type of maize, we think it necessary to give several geographical and agricultural interpretations of the observed facts. A study of the map [not in the original] of the geographical distribution of the described type of condensed, short plants will show that it is adapted to the driest regions, where agriculture is possible only under irrigation. It is also clear that this type of plant is adapted to the agricultural plains and lowlands. The expedition of the author in 1925, 1926, and in 1927, into Turkestan and Azerbaijan, and the expedition of E. A. Stoletova in 1925 and 1926 into Armenia completely and definitely attest to this fact.

In those regions in which the presence of the Persian type of maize was established, the maize fields are usually of very small area, since these regions are known to be essentially limited to the culture of cotton. Maize is here grown on the edges of cotton fields or as a kitchen-garden crop. The biological and agricultural description of the plant and the extraordinary adaptation of this crop plant to the diverse

conditions of the region of its cultivation were of great interest. Its shortness and its condensed structure are very valuable characters for regions of irrigation, giving a plant steadiness against the wind and protecting it from lodging on softened irrigated soil (see Kempton, 1921). The nearness of the leaves to each other, as effected by the shortness of the stem internodes, causes them to shade one another, by which, apparently, a reduction of transpiration is obtained. The stiffness of the leaf blades, oriented parallel to the sun's rays and not perpendicular to them, represents a broad adaptation in the plant kingdom without excessive insulation of the leaf in hot dry areas. The rough cutinized leaf which, unfortunately, was not studied anatomically, may also be considered an adaptation for reducing transpiration.

In 1927 during the journey to the Iolotansk Experiment Station in Turkmenistan, which is located on the edge of the burning waterless desert of Karakum, we chanced to see burned areas on the leaves of the American variety of maize in the variety observation plots. The burning was caused by the hot dry winds "garmsil", which are peculiar to the central Asian regions. In the local collections there were no similar burns. The panicles are covered by the stiff upper leaves and the silking ears are hidden in the axils and sheaths of the leaves. Thus these delicate flowering organs are protected from the destructive action of the dry burning winds of the Asian desert.

The simultaneous appearance of the male and female flowers, facilitating the timely utilization of the pollen, must be recognized as very expedient under the conditions of central Asia, for in the dry hot air the flowers and pollen of maize cannot be abundant, nor can the germinating pollen grains.

According to their reports, the American investigators consider the character *brachytic* to be very important, especially for dry regions, and are working towards a combination of the productiveness of normal types of maize with the shortness

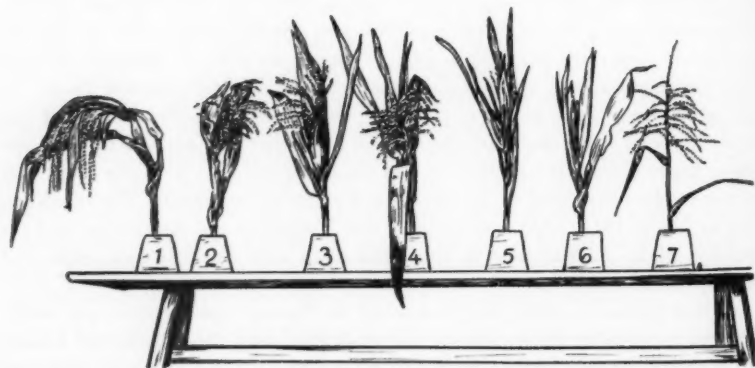


Fig. 11. Different types of covering of the panicle by the upper leaves. Plants 1 and 2, Primorskii Province; 3-6, Persia and Turkestan; 7, common open panicle. Kharkov, 1927.

of *brachytic*. In the collections described as the Persian type we have an undoubted approach to the resolution of this problem in that we have an entire array of other characters for the final stages of the important selection work to find a drought-resistant type of maize.

3. CONVERGENCE IN THE VEGETATIVE APPEARANCE OF THE PLANTS OF MAIZE AND SORGO ORIGINATING FROM THE SAME REGIONS OF ASIA

A great variety of crops which originated from widely different parts of the world were planted in 1927 at the Ukrainian Station of the Institute near Kharkov. These plants demonstrated that the place of geographical origin of many crops is mirrored in the array of general vegetative characters, notwithstanding the fact that they are classified in widely differing species, genera, and families. For example, the lucernes, flaxes, and wheats of north Africa are distinguished by a very intensive growth and differentiation in the early stages following germination. Flax, peas, and wheats from central Asia have a definite tendency toward dwarfness and slow growth in a number of collections. The lucerne of Turkestan has, in comparison with the lucernes of other regions, short internodes, slow growth, etc. Apparently, the ecological conditions which have been imposed on these crops in the current century have influenced them to the production of a general ecotype, the one most successfully responding to the conditions of the region.

While we were conducting a detailed study of a large collection of maize and sorgo in 1927 at the Ukrainian station of the Institute, in cooperation with V. I. Savron and A. I. Ivanov, we noted that a striking analogy was manifest in the aspect of the plants of maize and sorgo from the same regions of Asia. In the preceding section we described in detail, under the name *the Persian type*, a special type of maize which was distinguished by shortness in height and internodes. Maize, which is a new plant on the Asian continent, changed its aspect in central Asia in the very same direction as the oldest crops—flax, lucerne, etc. In the sorgo stocks A. I. Ivanov noted plants among the Turkestan collections which were distinguished by the very same short stems and broad leaves as were previously described for maize of the Persian type (fig. 12).

During our expedition to Turkestan in 1927, in cooperation with I. V. Gduzenko, we observed a striking resemblance in vegetative aspect between the plants of maize and sorghum in the field. In this respect the Geoktepe region of Turkmenistan is especially interesting. The very same short height was seen in sorghum in fields of the Shirabude Experiment Station near Bokhara. This dwarf sorghum is considerably less widely distributed in Turkestan than the common tall type, but we discovered it, nevertheless, in many places, in many regions (Geoktepe, Archman, Termez, Merv, etc.). In these same regions and places we almost always discovered the dwarf, condensed Persian type of maize plants.

In other regions of Asia—Manchuria, northern China, and the Primorskii Province—there was also a striking resemblance in vegetative aspect between maize and sorgo which originated from the same region. Plots of maize and sorgo are



Fig. 12. Sorghum and maize plants of short habit, from Bokhara, 1927.

already quite striking in appearance at the 9–10-leaf stage, being sufficiently distinguished by tall plants with thin stems, long basal internodes, and a palm-like arrangement of their long, narrow leaves at the apex (fig. 13). These plots all contained plants from Manchuria, northern China, and the Primorskii Province. Further observations showed that, besides sorgho and maize, the same plant structure may be observed in plots of *Panicum italicum* from the same regions.

Upon further development the similarity between these plants is not diminished: Manchurian Kaoliang resembles Manchurian and Primorskii maize, and Manchurian and Primorskii maize are similar in aspect to Kaoliang. Figure 14 represents maize and sorgho from central and eastern Asia, photographed after flowering. The similarity is striking. In these two regions sorgho and maize are so similar in external aspects that an inexperienced observer recognized sorghum plants of these regions by their outward aspect without difficulty, after once seeing our plots of the peculiar maize of central and eastern Asia. In addition to the illustration, we present measurements of the internodes of the plants which were photographed, numbering the internodes from bottom to top (Table IX).

The data presented here corroborate well what was stated in the text and demonstrated in the illustrations. The facts which have been studied in this section lead involuntarily toward the raising of several general questions of the biology and variation of plants. For instance, *Andropogon sorghum* presents an Asiatic

TABLE IX
INTERNODE LENGTHS (IN CM.) IN PLANTS OF SORGHUM AND MAIZE IN FIG. 15,
GROWN AT KHARKOV, 1927

Number of internodes	Sorghum Bokhara	Maize Termez	Manchuria	
			Sorghum	Maize
1	2.0	2.0	4.0	6.0
2	2.5	3.5	11.0	8.0
3	3.75	4.0	21.0	8.5
4	3.75	6.5	27.5	20.0
5	4.0	3.25	24.5	22.5
6	4.5	5.5	24.5	19.0
7	4.0	4.0	27.0	21.0
8	4.0	3.3	29.5	18.5
			(to panicle)	
9	5.0	5.0	49.5	18.0
10	5.0	4.5		
11	5.0	10.0		
12	5.0	9.0		
	(to panicle)			
13	15.0	8.0		
14		2.0		
15		1.5		
16		8.0		
(to panicle)		(to panicle)		
17		9.0		

aspect, having been known to be in culture in Asia for more than 3,000 years. Also maize, according to the present view, could not have been introduced into Asia earlier than 1516, when the Portuguese ships first touched the China shores. Thus, 400 years is the maximum time which, on the basis of the literature, can be assumed for the cultivation of maize in Asia. In an evolutionary sense it is impossible to consider 400 years a long time, but meanwhile, during these 400 years, maize, which is foreign to the Asiatic continent, attained an aspect similar to that of the oldest crop plant in Asia—sorgo. On the basis of these observations we must assume either a very high plasticity for the maize plant, or conversely, that maize was introduced into Asia earlier than 1516. Unfortunately, due to insufficient data, the latter is an impossible assumption.

4. LIGULELESS MAIZE

A peculiar condition of leaves which lack a ligule at the juncture of the leaf sheath and the blade has been described in cereals by several authors. Nilsson-Ehle observed it in oats; N. I. Vavilov discovered liguleless type of rye and wheat in Pamir; K. A. Flaxberger established the presence of liguleless wheats in collections from the island of Cyprus (Flaxberger, 1926). Liguleless maize was described by Emerson (1912). Liguleless plants were discovered by him in 1910 in the progeny



Fig. 13. Similarity of plant habit in sorghum, maize, and *Panicum italicum* from Manchuria, in the 9- to 11-leaf stage. [From left to right]: maize, *P. italicum*, sorghum. Kharkov, 1927.

of a self-pollinated plant which was grown from a single ear with tooth-like kernels which was brought from the National Corn Show in Omaha. A closer inspection of the leaves of the *liguleless* plants showed that, besides the reduction of the ligule (which in several leaves is retained although in a very rudimentary form), the auricles, by which the vertical position of the leaves and their clasping of the stem is actually accomplished, are also absent.

A genetical investigation of the character *liguleless* demonstrated that it is recessive and in hybrids segregates in a ratio of 3:1. As far as we know, no one besides Emerson has studied the character of ligulelessness in maize. In 1927 at Kharkov in our plots, V. I. Savron and I discovered ligulelessness in plants of maize in three cases:



Fig. 14. Convergence in vegetative habit of maize and sorghum from central and eastern Asia. Center, a plant of *P. italicum* from Manchuria. Kharkov, 1927.

1. Collection no. 2773 from the village of Seraphimovok, the Vladivostok district in the Primorskii Province, referred to the group *everta*. Among 20 plants of a plot, in 11 the leaves on different stems were marked by a reduction of the ligules from complete absence to its retention as a rudiment as compared with the normal aspect. The auricles were absent from the leaves. In fig. 16 this original plant type is depicted.

2. Collection no. 2746 from the village of Novopokrovok, in the Spassk district, the Primorskii Province. Of 22 plants only one was liguleless, but the ligulelessness was very well developed.

3. Collection no. 1419, originating from the Caucasus (unfortunately without a more exact notation as to place, and doubtful as to origin). Of four plants, one was typical liguleless.

Liguleless plants were not discovered in any other collections either at Sukhum or Kharkov, notwithstanding the fact that the collection was world-wide. Also, in general, no one has established ligulelessness before in open-pollinated collections of maize under natural conditions of development. Our findings appear to be peculiar in their class and the maize of Asia is of new interest.

Collections nos. 2773 and 2746 were received from the Primorskii Province the first of the year 1927, and were first seeded in 1927. The origin of collection no. 1419 is not certain, but the original seed of it was used for sowing.



Fig. 15. Maize and sorghum stems with the leaf sheaths removed, from Bokhara and Manchuria. Kharkov, 1927.



Fig. 16. Liguleless plant in collection 2773 from the Primorskii Province, near Vladivostok. Kharkov, 1927.

III. GENERAL CONCLUSIONS CONCERNING THE MAIZE OF ASIA

In the preceding section, on the basis of data from the literature and from our own investigations, we arrived at the conclusion that in the maizes of Asia we have observed an array of characters and peculiarities which are unknown in America, or which are extremely rare in America. At any rate, we observed these characters, not in occasional isolated instances but often and associated with definite and frequently large areas. Therefore, waxy endosperm has a wide distribution in eastern Asia from 5–45° north latitude; dwarf plants are peculiar to vast areas of central Asia; while the sheltering of the panicles by the upper leaves and the concealment of the silking ears in the leaf sheaths are encountered in eastern and central Asia, Transcaucasia, etc.

These facts indicate that in Asia several conditions contribute to the production of new types of this plant which is known to be American. However, when we

appraise more closely the characters which are peculiar to the maizes of Asia or discovered in them, we should, on the basis of the data from the literature, meet recessiveness in most of them. Thus waxy endosperm, *brachytic* dwarfness of the plant habit, and ligulelessness are recessive.

In 1927 N. I. Vavilov published a very interesting work on the geographical regularity in the distribution of genes of the crop plants. In the words of N. I. Vavilov: "The basic centers of diversity of types are the sources of diversity which are characterized not only by the presence of a large number of types, but, what is no less important, by the presence of a large number of dominant factors. Conversely, the secondary centers of diversity are characterized by a diversity principally of recessive factors."

From this viewpoint concerning the maize of Asia we undoubtedly have a secondary center of diversity, and our Asiatic material gives satisfactory facts for the corroboration of the views of N. I. Vavilov. At the present time no one doubts the American origin of maize (Messadaglia, 1924; Weatherwax, 1923) [And a reference to a non-existent sixteenth item in his *literature cited*], and the Asian maize is of course viewed as an introduction.

This assertion by no means hinders the raising of another exceedingly interesting question, and this question concerns the time of introduction of maize into Asia. At present we have no documentary evidence which would indicate that maize was known in Asia before Columbus [A reference to a non-existent seventeenth citation]. But the striking facts which are described in the present paper inevitably lead to the idea that Asian maize, if it be not viewed as native, at any rate is very ancient. These characters, which were seen in Asiatic maize, attest to this explanation. As we saw, waxy endosperm, which was discovered in Asiatic maize, was also discovered in the most ancient crop of Asia—sorgo. Dwarfness, which is characteristic of Asiatic maize, is also characteristic of sorgo, flax, and other ancient crops. But these characters are found in large areas, and for them to be manifest in maize, time, of course, is required.

If we agree with Collins, we must assume that waxy endosperm arose in the maizes of Asia by means of mutation and has its place of origin in upper Burma, which is largely populated by wild tribes with whom even today it is almost impossible for aliens to have intercourse. Now, concerning the time interval in question, we must understand when and how maize could have been removed from America into this isolated wild land, given there a mutation and as a mutant diffused from the Philippines to northern Manchuria. The answers we can not give, of course, with certainty, but as a conjecture we should suppose that likely there was an earlier cultivation of maize in Asia than the time of the first landing by the Portugese on the shores of Asia in 1516. A similar conjecture was expressed in one of his papers by Collins (1909), but subsequently he retracted it. The facts, which were established by us, return us anew to this supposition and this time with a great deal of conviction.

We have already dwelt upon the agricultural and biological significance of these characters which were described for Asian maize. Their value as to suitability to the exceptionally dry conditions of central Asia is undoubted, and therefore Asiatic maize arouses a very great interest regarding plant breeders' aims. The character *waxy* is no less interesting from the practical point of view. The exceptional capacity of waxy endosperm to be hydrolyzed by the diastase enzyme has been explained according to the most recent investigations of Americans. In comparison with other types of endosperm, the hydrolysis of waxy endosperm is more rapid in several cases [Reference to literature citation 18].

This condition leads one to suppose an increasing adoption of the products prepared from waxy maize in the diet of the natives. We do not yet know the suitable experiments, and we know nothing about the conduction of plant-breeding experiments with waxy maize, but both [questions] arouse very great interest.

Rapid-growing races of waxy maize from the Primorskii Province and northern Manchuria ripened fully under the conditions of Kharkov, and subsequently in almost the entire maize-growing region of the USSR.

The present communication represents in part the large cooperative work on the investigation of maize and sorgho which is being conducted by the author in cooperation with I. V. Kozhukhov, M. I. Hajinov, V. I. Savron, A. I. Ivanov, and E. S. Yakushevskii at the All-Union Institute of Applied Botany. We must also mention the exceptional aid which was rendered by the section of M. G. Tsyup in photographing the most interesting plants. We express also our deep gratitude to all the institutions and persons who responded to the requests of the section and sent to the Institute collections which served in a large part as material for the present paper.

Leningrad.

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LADYFINGER AND TOM THUMB, TWO OLD VARIETIES OF POPCORN

EDGAR ANDERSON

Missouri Botanical Garden and Washington University

AND WILLIAM L. BROWN

Department of Plant Breeding, Pioneer Hi-Bred Corn Company

Two very different varieties of popcorn, Ladyfinger and Tom Thumb,¹ have been extensively confused in agronomic and genetic literature. While the correct naming of popcorn varieties is a matter rather outside the ordinary realm of scientific endeavor, these two varieties have been so frequently used in genetic and breeding experiments, East (1911), White (1917), and Kempton (1926), that it seems worth while to describe and differentiate them. Aside from small kernels and small cobs the two have almost nothing in common. Each represents a morphologically extreme type among the readily available United States varieties of *Zea Mays*; for that very reason both may be of potential importance in practical breeding programs as maize breeding becomes even more scientifically expert.

A few of the outstanding differences between these two varieties are shown in Table I. Even though the varieties have been confused because both have small ears and small kernels, they are readily distinguishable even by these characters. Ladyfinger has smaller kernels than does Tom Thumb and they are a straw-yellow rather than a butter yellow. The ear of Ladyfinger does indeed suggest a finger, being slender and straight-sided, while the ear of Tom Thumb, though usually even shorter, tapers from the center to both ends, like a miniature barrel.

In growth habit the two varieties are diametrically different. Tom Thumb is the earliest of early varieties and does not grow into a normal plant south of the northernmost tier of states. In most of its characters it is a typical northern flint (Brown and Anderson, 1947). It has one or two ears on the main stalk when grown in southern Minnesota. It tillers readily and the tillers are inferior to the main stalk. The foliage is a yellowish-green and the tassel has few and slender branches. Ladyfinger is the latest variety of any kind of maize in most of the gardens in which it grows. Its growth habit is like that of Oriental Popcorns (Stonor and Anderson, 1949): it develops slowly; its leaves are upright; the internodes are short; it may have 5 to 7 ears on the main stalk. It tillers abundantly and the tillers are subequal to the main stalk in size and appearance (pl. 12, fig. A). The tassel, though small, has many branches and is scarcely exerted from the upper leaves.

¹In discussing these two varieties we have used the oldest names in the literature, the more readily since they are appropriate names and since they have been widely used for these varieties at one time or another. Ladyfinger has been very extensively referred to, not only as Tom Thumb but as Australian Hull-less. The latter name, however, seems to have been even more widely applied to varieties which apparently came from crosses between Ladyfinger and some variety with a higher row number. The name Tom Thumb has been applied not only to Ladyfinger but also to various small-eared popcorns, including pointed-kernel types which morphologically are very different from the Tom Thumb herein described.

TABLE I
TABULATION OF OUTSTANDING DIFFERENCES BETWEEN TOM THUMB AND
LADYFINGER POPCORNS

	Tom Thumb	Ladyfinger
Season	Very early	Very late
Ear shape	Small, barrel-shaped	Small, finger-shaped
Kernel color	Deep yellow	Pale yellow
Tassel	Few branches; exerted from leaves	Many branches; tassel surrounded by upper leaves
Leaves	Yellowish-green	Bluish-green, upright
Internodes	Few; upper ones elongated	Many; upper internodes very short

Little is known of the history of either variety though both have been commonly grown under various names and both have been used in popcorn breeding for over fifty years. Eldredge (Eldredge and Lyerly, 1943) described both varieties as among the types of Tom Thumb popcorns which he found when assembling material for his popcorn-breeding program.

Though little is known about the agronomic history of Ladyfinger the facts suggest that it may be one of the oldest varieties of maize. It is strikingly similar to varieties of popcorn obtained from pre-Columbian graves in Chile and Peru. Varieties somewhat resembling it have been obtained from scattered localities in South America and, as mentioned above, it is generally similar to the popcorns collected among the primitive Naga tribes of Assam by Stonor. Though we do not know how or when it reached the United States, we do know that it has been here over a century. A detailed description of it by Ebenezer Emmons in 1849, leaves no room for doubt that it was this very same variety to which he gave the name of Ladyfinger in his survey of the maize varieties in New York State (p. 265):

"Illinois or Ladyfinger corn. Pale yellow. Ear small, slender, and tapering. Rows 12. Kernels small, pointed, rounded upon the back. It is an unproductive kind, bearing sometimes four ears upon a stalk, but the stalk is from 7 to 8 feet high. It is a late kind . . ."

Ladyfinger is a high-quality popcorn. Though small and comparatively flavorless, it is delicate in texture and is almost completely devoid of the roughage which some people find so objectionable in most other popcorns. It is this high quality which has preserved it in spite of its lateness and rather low yield. We have frequently found it being grown by small seedsmen or in home gardens. Inquiry as to where it had been obtained has always produced a similar story. Some friend or relative found it to be of such high quality that it was recommended as being worth while in spite of its lateness. In the few cases where we were able to go back one step farther we learned that the previous grower had himself obtained it in just such a fashion.

Ladyfinger has evidently been used considerably in popcorn breeding. We found the first-generation hybrid between it and Japanese Hull-less types to be high both in quality and yield. Various blends of the two varieties are, or have been, under cultivation but those which we have grown show a strong tendency to revert back to the original Ladyfinger type.

About Tom Thumb we know even less. In its growth habit it is so similar to the early small-eared northern flint varieties such as those grown by the Micmac Indians that it would seem to be either a northern Indian variety or one produced by crossing some other popcorn with one of these varieties.

In our collections are specimen ears, some of them going back to the first decade of the twentieth century from several localities in eastern north America. Modern popcorn breeding has driven it almost out of existence. From Professor Wiggins of Cornell we obtained a very early inbred derived from this variety or one of its hybrids. We were not, however, able to obtain viable seed of the open-pollinated variety until we finally located a stock at the Montreal Botanical Garden where the superintendent, Henri Teuscher, had been growing it for some years. Because of its scientific value this was increased for us by William Landgren of Willmar, Minnesota, and will be generally available for scientific or practical experiments.

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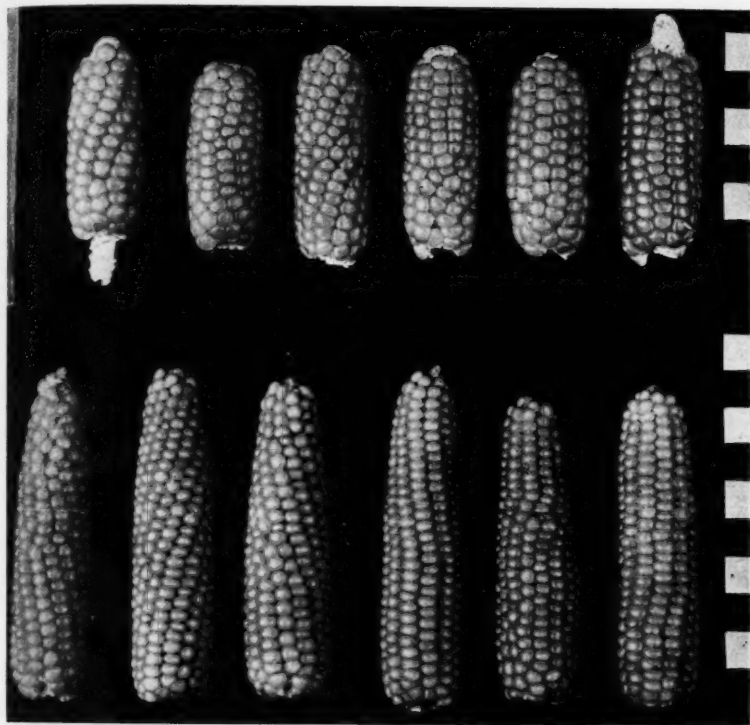
EXPLANATION OF PLATE

PLATE 12

Fig. A. Above, 6 ears of Tom Thumb; below 6 ears of Ladyfinger. Scale at the right in centimeters.

Fig. B. Close-up of tassel of Tom Thumb. Line is the same width as those in the background of Ladyfinger illustration.

Fig. C. Typical plant of Ladyfinger. Tracing of leaf blade at the left. Background ruled in lines 25 cm. apart.



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ANDERSON AND BROWN—OLD POPCORN VARIETIES

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A FIELD SURVEY OF CHROMOSOME NUMBERS IN THE SPECIES OF *TRADESCANTIA* CLOSELY ALLIED TO *TRADESCANTIA VIRGINIANA*

EDGAR ANDERSON

PART I. PRESENTATION OF DATA

Some twenty years ago I began to collect quantitative data on variation in chromosome number in *Tradescantia*. Having learned at the John Innes Horticultural Institution the comparative ease with which accurate chromosome counts of the American *Tradescantias* could be made with modern methods, and living within easy-collecting distance of five different species, I set about to supplement the extensive chromosome-number surveys of various other cytologists by an intensive survey of a few species. Darlington (1929) had shown that chromosome number *could* vary in this group of species; I thought it would be productive to learn to what extent it actually did vary. This eventually led to taxonomic (Anderson and Woodson, 1935) and cytological monographs (Anderson and Sax, 1936) with Dr. R. E. Woodson, Jr. and with Dr. Karl Sax in which I undertook the major responsibility for building up a comprehensive collection of living plants while my colleagues performed the bulk of the technical investigations. When still actively engaged upon the survey I stumbled upon the phenomenon of introgression. Before the survey was completed I had moved from the Missouri Botanical Garden to Harvard University and then moved back again. In spite of these diversions the survey has proceeded. Chromosome numbers have been carefully determined for nearly 1000 plants of eighteen species of *Tradescantia* in the *virginiana* group, all of them collected in the field. Nearly 500 of these counts have been accurately recorded and filed and are presented herewith. They give good, quantitative data on the stability of chromosome number under field conditions. Preliminary accounts were included in the cytological and taxonomic monographs, and a summary of some of the main points was included in a survey article in the *Botanical Review* (Anderson, 1937). Detailed reports have been made on various special phases of the investigation (Anderson, 1936; Anderson and Diehl, 1932; Anderson and Hubricht, 1938; Riley, 1936; Whitaker, 1939). This constitutes a final report on the original project. In presenting the cytological data for each species, I have therefore included additions and corrections to the cytological and taxonomic monographs, as well as notes and comments on each species as an evolutionary unit.

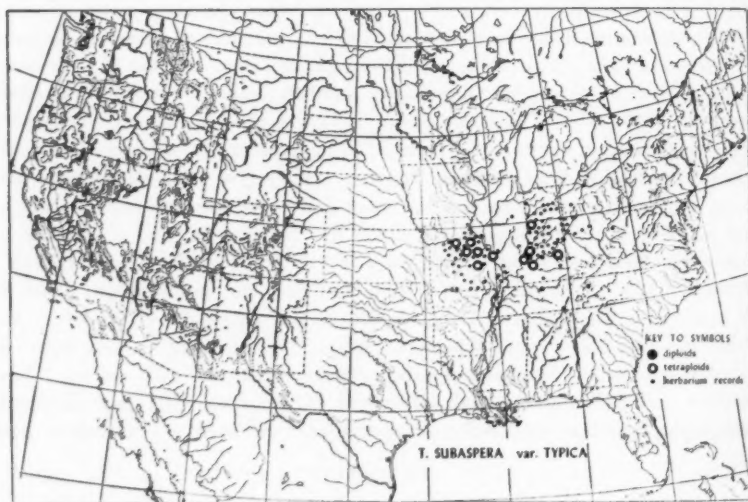
METHODS

Counts were made both in the field and the experimental plot. They were made almost exclusively from fresh aceto-carminic smears. Wherever possible metaphases of both meiosis and mitosis of the microspores were examined. Any seeming irregularities of either of these divisions were exhaustively looked into. If the microspores showed any micronuclei or if the percentages of sterile pollen were higher than normal, meioses were obtained for study even though this meant transplanting to an experimental plot and re-investigating the plant in another season.

Counts were made in the field or on transplants of my own collecting and on plants sent in by friends and collaborators. The technique of labelling and indexing these collections has been described in detail in Anderson and Sax (1936).

PRESENTATION OF DATA

The species are presented here in the same order as the taxonomic monograph by Anderson and Woodson: *T. subaspera*, *T. edwardsiana*, *T. ozarkana*, *T. ernestiana*, *T. virginiana*, *T. hirsutiflora*, *T. tharpii*, *T. gigantea*, *T. obiensis*, (*T. reflexa*, *T. canaliculata*), *T. paludosa*, *T. bracteata*, *T. hirsuticaulis*, *T. longipes*, *T. reverchonii*, *T. humilis*, *T. subacaulis*, *T. roseolens*, *T. occidentalis*. These are all in the *virginiana* group and represent all the known species of that group native to the United States. They all have erect or ascending stems, not ordinarily rooting at the nodes (see comments under *T. paludosa*). The sepals are more or less concave but are without a definite keel. The bracts below the flowers are conspicuous and similar to the leaves. The seeds are somewhat oblong with a linear funicular scar as long as the seed. The chromosomes are large with median or submedian attachment constrictions. The chromosome number ($2n$) is normally either 12 or 24.



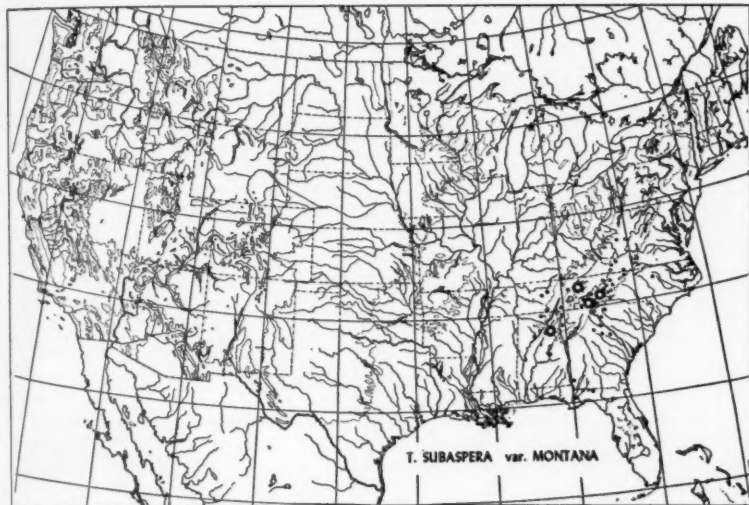
Map 1

Tradescantia subaspera var. *typica*.—

This has been sampled at twelve localities from northern Florida to central Missouri. At Wolf Creek, in eastern Tennessee, one diploid ($2n = 12$) was collected. The 16 other plants, from the eleven other localities, were all tetraploid

($2n = 24$). No plants were found with extra chromosomes, with fragment chromosomes, or other cytological abnormalities.

T. subaspera var. *typica* is a handsome, summer-blooming plant of deep shade and rich soils which in its general appearance is quite unlike the other species of this group. The record in northern Illinois in Anderson and Woodson was in error. The common so-called *T. virginiana* of gardens is descended almost as much from this species as from true *T. virginiana*.

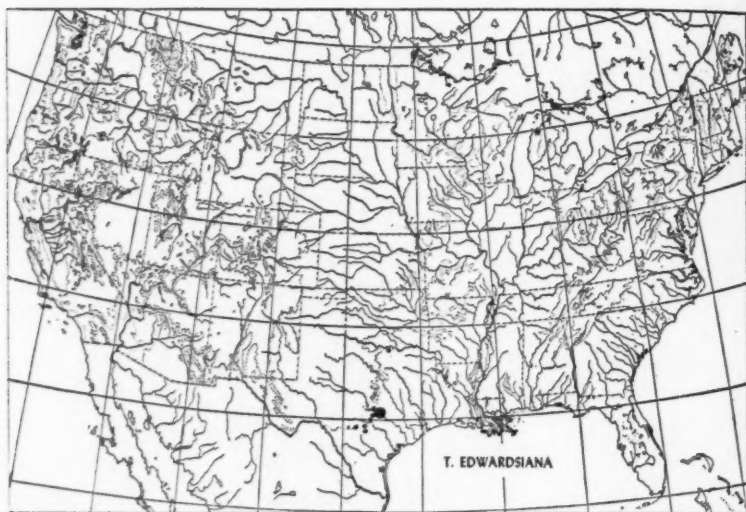


Map 2

Tradescantia subaspera var. *montana*.—

Morphologically, this variable taxon is similar to artificial hybrids between *T. subaspera* var. *typica* and *T. obiensis*. Hybridization with the latter species is still actively going on, particularly in habitats grossly disturbed by man, and two of these are reported below. *T. subaspera* var. *montana* is so variable and has so much higher a percentage of sterile pollen and cytological abnormalities than any of the other taxa reported on here, that it seems likely it is the result of introgression of *T. obiensis* into *T. subaspera* var. *typica*. Though much of this introgression may have occurred recently it was the opinion of Dr. Hiram Showalter, who was studying the phenomenon at the time of his death, that part of it was pre-Columbian. A careful study of *T. subaspera* var. *montana* in the field and in the breeding plot would settle this question and be of general interest. I have Dr. Showalter's notes and herbarium specimens, as well as a few of my own, and shall be glad to turn them over to any qualified person with the facilities for continuing with the problem.

Collections were made at eight localities, from Alabama to Tennessee and North Carolina. Chromosome counts were made on 25 plants in all. Twenty-four of these were regular tetraploids with 24 chromosomes. The other plant had two extra chromosomes; it showed a high percentage of bivalents at meiosis; and the microspores contained occasional micro-nuclei.



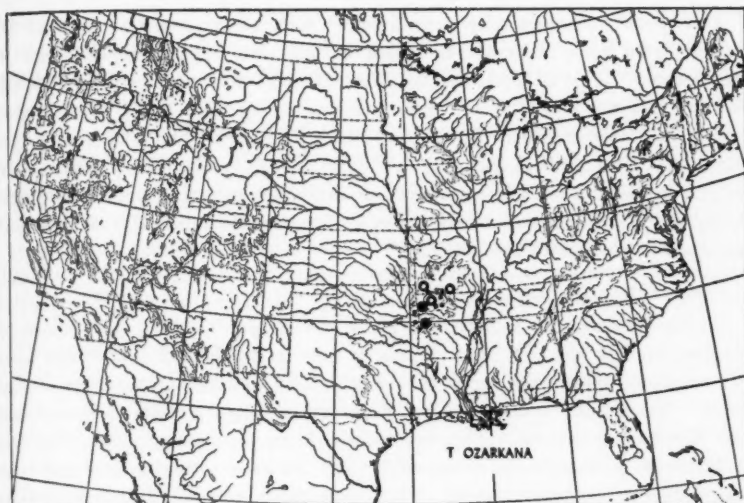
Map 3

Tradescantia edwardsiana.—

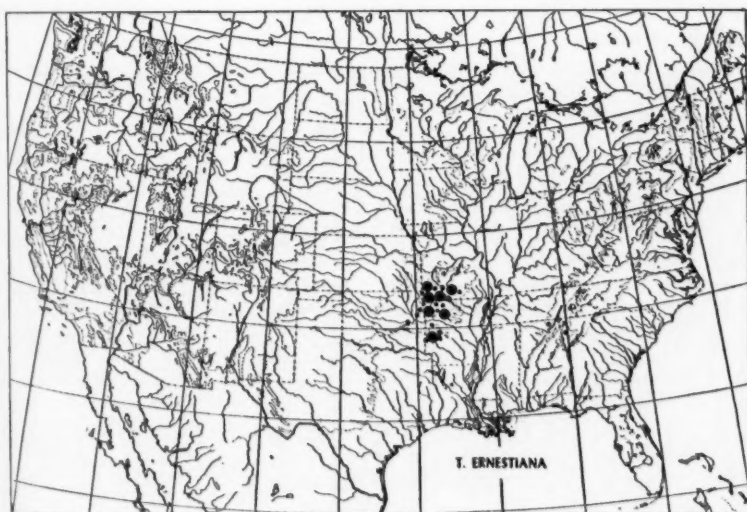
This is a very localized species growing in shady spots along the edge of the Edwards Plateau. Additional collecting has extended the range to northern Texas. Collections were made at two points; 17 plants were examined. All were regular diploids with 12 chromosomes.

Tradescantia ozarkana.—

This peculiar species has a disjunct distribution on isolated Cretaceous mesas and plateaus in Arkansas and southwestern Missouri. Additional collecting has slightly extended the range. At the most southwestern part of its range (Rich Mountain) this species is diploid. In the Boston Mountains and in the Ozarks it is a tetraploid. Counts were made on one plant each from five localities. All were regular tetraploids or regular diploids with no extra chromosomes or other cytological abnormalities. In southwestern Missouri, at the type locality for the species, it is undergoing extensive introgression from *T. obiensis*.



Map 4



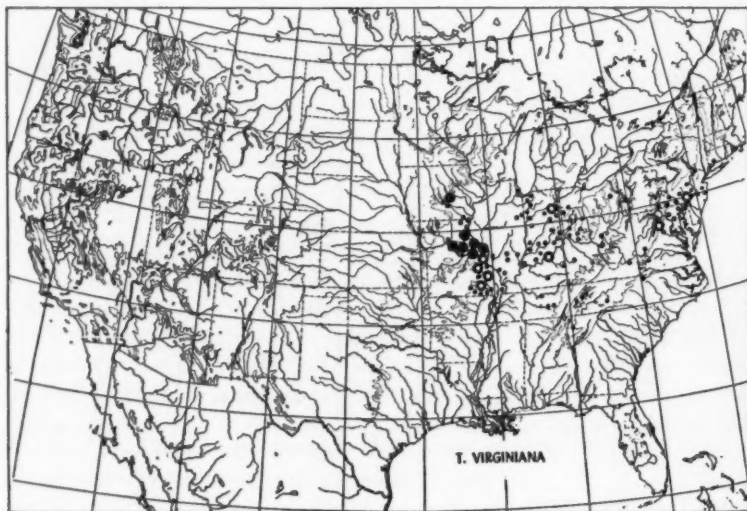
Map 5

Tradescantia ernestiana.—

This species is known only as a diploid. Nine counts were obtained at five localities from Rich Mountain to Missouri. All were regular diploids with 12 chromosomes ($2n$). *T. ernestiana* has a distribution similar to *T. ozarkana* though these two species are very unlike. Additional collecting and a better understanding of the species have extended the range to northern Alabama and northern Georgia, a range which is typical of many species found in the Ouachita Mountains. Specimen plants from northern Alabama sent us during the early years of our investigation by Dr. B. P. Kauffmann, and which we were unable to identify at that time, undoubtedly belonged to this species.

Tradescantia virginiana.—

During its career as a cultivated plant this species has been so modified by hybridization and selection that the plants now in cultivation under that name are completely outside the range of variation of the native populations of that species. This matter is discussed below at greater length. The previous record from Wisconsin is in error. The records from Michigan, Massachusetts, Vermont, and Maine are of garden plants run wild. The species is a regular tetraploid from Pennsylvania to southern Missouri. I have recorded counts on 16 individuals from eleven localities. One plant from De Soto, Missouri, was a tetraploid with 2 extra chromosomes. In the diploid area in northern Missouri and adjacent Illinois and Iowa we have counts on 18 plants from eleven localities. Seventeen of them are regular diploids; the other plant had 2 small fragment chromosomes which paired regularly at meiosis.

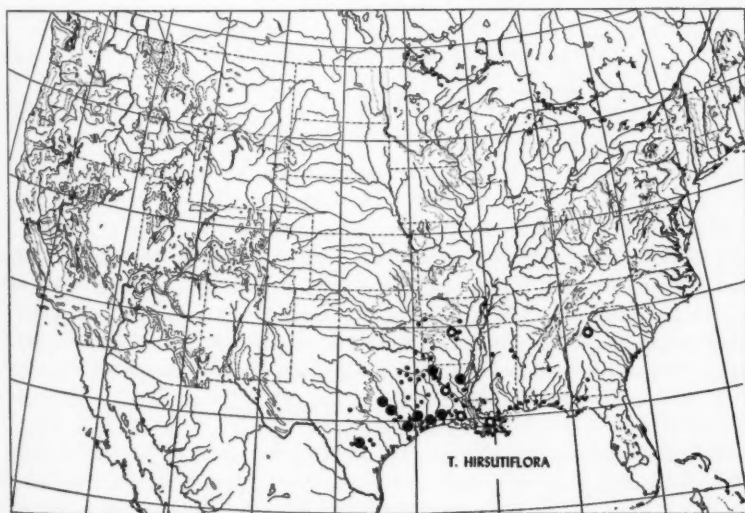


Map 6

The diploid zone of this now prevailing tetraploid species is of some interest floristically. It includes the small area north of the Missouri River and west of the Mississippi which apparently was not over-run by either the Illinoian or Kansan glaciation. It is a region so rich in species which are rare or unknown in the glaciated areas immediately around it that Steyermark and others (Steyermark, 1934; Steyermark and Palmer, 1935) have supposed its floristic composition reflects its physiographic history. The fact that all the *T. virginiana*'s which have been examined in this area are diploids, while the species is prevailing tetraploid, would lend some support to this theory. The diploids, almost certainly the original form of the species, might have persisted here when eradicated elsewhere or their habitat might have retained its essential features here in the absence of glaciation though so altered in the glaciated areas that the diploids never spread back in.

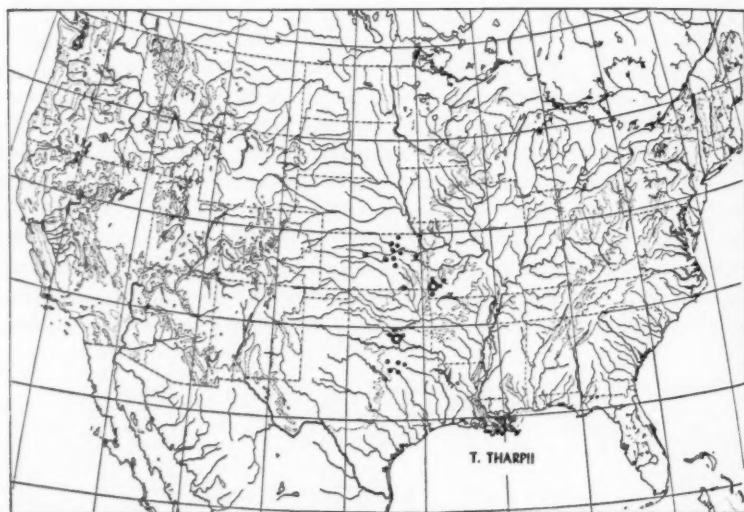
Tradescantia hirsutiflora.—

This is the least understood of any of the species in the *virginiana* group. Its members were originally native to light soils from Texas to Florida. Most of the habitats in which it originally flourished have been put under cultivation. Collections by Demaree have extended the distribution into central Arkansas. Introgression with several other species has taken place extensively, notably with *occidentalis*, *obiensis*, and *paludosa*. Some of the introgressants are at a selective advantage in the new habitats, being under man's influence, and *T. hirsutiflora* is on its way to becoming a common weed in parts of the South. It, or something very closely akin to it, became incorporated in *T. bracteata*, forming a binary



Map 7

variation pattern which was the subject of a special study (Anderson and Hubricht, 1938). The weedy nature of *T. birsutiflora* is reflected in the high percentage of cytological abnormalities which have been found in the relatively few populations which were examined. There is a diploid area in Texas and Louisiana, while as a tetraploid the species has spread north to central Arkansas and east to Georgia. The diploid has been studied at twelve localities. Twenty plants had no irregularities. Two had each an extra pair of chromosomes and one showed a large fragment chromosome at meiosis. Tetraploids were studied at four localities, one example from the same Louisiana parish as a known diploid. Chromosome counts were made on five plants. All were regular.



Map 8

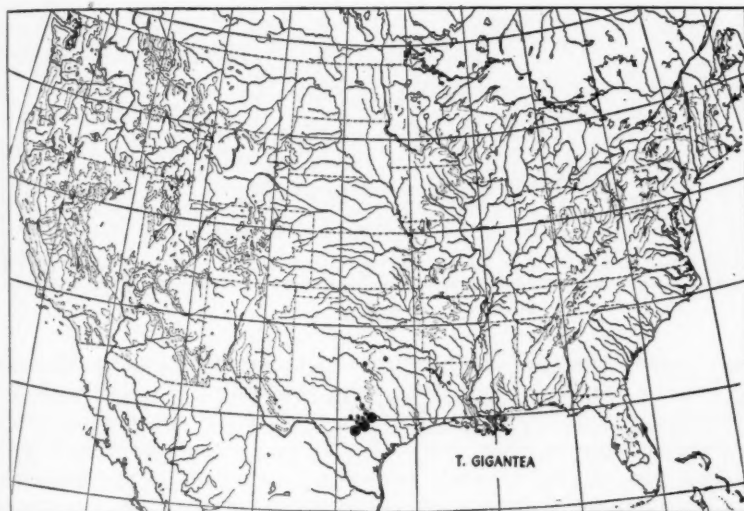
Tradescantia tharpiana.—

This charming and distinctive species is native to the front of the Great Plains from Texas to Kansas. The record from eastern Oklahoma (Anderson and Woodson, 1935) is in error. In addition to an early count from a plant collected somewhere in Texas, we have counts from one collection each in Oklahoma, southwestern Missouri, and Kansas. All seven plants were regular tetraploids.

Tradescantia gigantea.—

This distinctive species, characterized among other things by a velvety pubescence on the bracts, was originally native to rocky places along the front of the Edwards Plateau. It has hybridized somewhat with the other species in that area and is now spreading out actively along railroad right-of-ways, roadsides, and

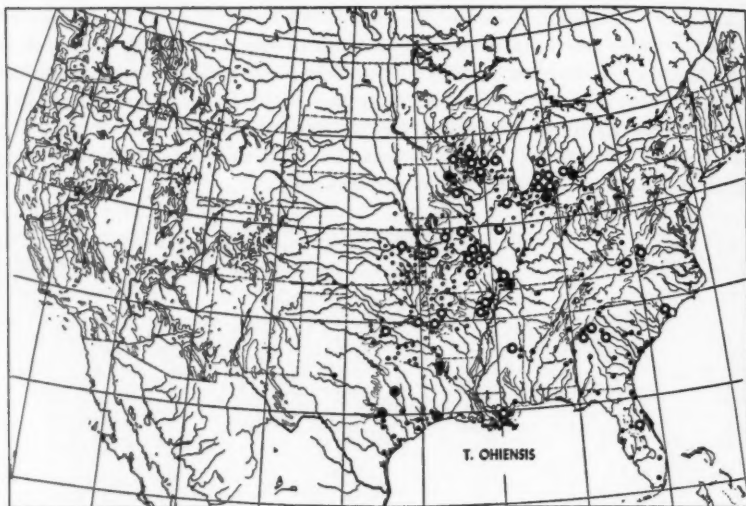
vacant lots. Additional collection has shown the range to extend into northern Texas. It shows marked resemblances to Mexican species which do not reach the United States. In common with *T. obiensis* it exhibits a character of considerable phylogenetic significance in the Commelinaceae; it has multiple cymes within its large floral bracts, instead of simple cymes like most of the American species. There are counts on 70 plants from twelve localities. All were regular diploids except one plant which had an extra pair of chromosomes.



Map 9

Tradescantia obiensis.—

This common, widespread species of the Middle West and the South has unfortunately gone by more than one name. It was referred to as *T. reflexa* in the 7th edition of Gray's *Manual* and as *T. canaliculata* in the monograph by Anderson and Woodson. *T. obiensis* is an older name and the correct one (Fernald, 1944) according to international rules. It has a diploid area in Texas and Louisiana and another in Michigan and Indiana which has been the subject of monographic attention by Dean (1954). No irregularities were found among the diploids. Among the tetraploids three plants with extra pairs of chromosomes were found, one in Mississippi, one in Florida, and one in Arkansas. The Mississippi plant showed a marked excess of non-disjunctional divisions at meiosis; five other plants from the same locality were normal. The exceptional plant from Clarksville, Arkansas, exhibited many micronuclei which did not disjoin properly. One plant from Hamburg, Missouri, in a colony suffering extensive introgression from *T. subaspera*,

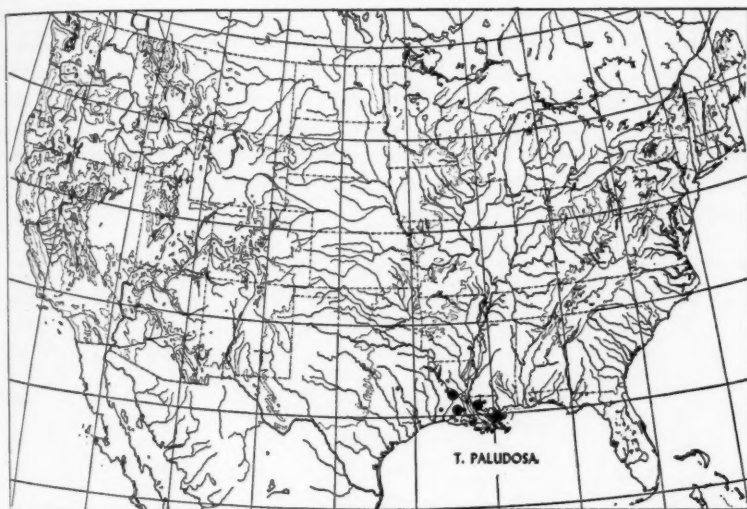


Map 10

showed many micronuclei in the microspores. One plant from Baraboo, Wisconsin, had irregular meiosis with univalents, a high percentage of non-disjunction, etc. In addition to these four plants showing irregularities of one kind or another, chromosome counts on regular tetraploids were obtained from 96 plants from 56 localities. In spite of its weedy tendencies, in spite of its auto-tetraploidy, this species for which we have a really significant sample shows only 4 per cent of obvious irregularities. All the records from the Virginia border northeastward are undoubtedly from introduced plants. The two collections from northern Michigan were apparently waifs. The species has never been re-collected in that area.

Tradescantia paludosa.—

This curious little species is native to rich Live Oak soils of the Mississippi Delta. Additional collection has extended the range of this species into southern Arkansas and eastern Texas on the same black-soil, low river-terraces from which it had previously been reported. It bears a curious morphological relationship to all the other species of the *virginiana* group. It differs very slightly from *T. obiensis*. However, the slight differences between it and that species are all in the direction of the creeping tropical *Tradescantias*. In other words, the differences, slight as they are, would almost remove it from this group of species. It has smaller flowers, is without stomata on the upper side of its leaves, and Bramsch (1936) has shown that, unlike the other species of the *virginiana* group, it resembles the tropical *Tradescantias* in the large cells on the upper sides of the leaves. It also comes closer to rooting at the nodes than any other species of the *virginiana* group, close enough so that it can be rooted readily from cuttings.



Map 11

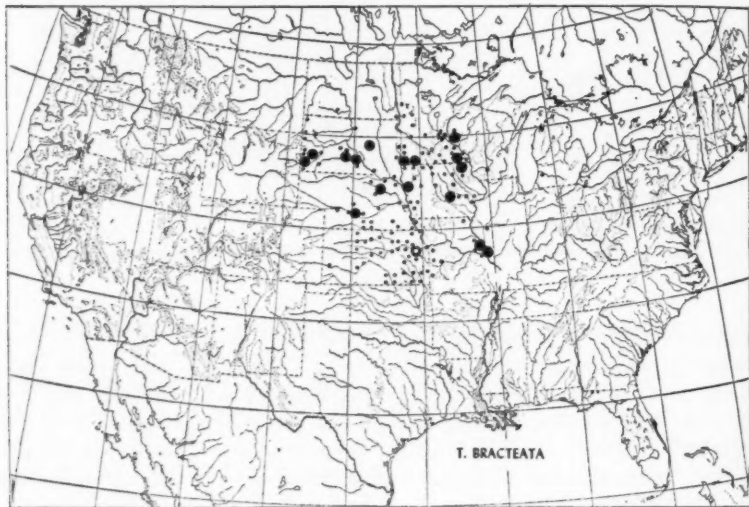
It seems to me quite probable that *T. paludosa* originated from a rare cross between *T. obiensis* and some tropical creeping *Tradescantia*, this hybrid backcrossing to *T. obiensis* and producing introgressants which eventually stabilized with a very few segments (perhaps one or two chromosome arms) in what was otherwise *T. obiensis*. The combination, however achieved, has been a boon to cytology. It combines the large, easily studied chromosomes of the *virginiana* group with the adaptability to greenhouse conditions of many tropical *Tradescantias*. It has become one of the standard subjects in radiation research and is one of several unexpected by-products of this investigation of chromosome-number variation.

T. paludosa is known only as a diploid. We have counts on 16 plants from four different Louisiana parishes. All these plants are regular diploids. Earlier collections were made by me from semi-domesticated plants in New Orleans gardens and from a population in the railroad yards which was hybridizing with *T. hirsutiflora* and became the object of a special investigation by Riley (1939). These were likewise diploids, but many plants among them had tiny fragment chromosomes, sometimes in very large numbers. These fragments have been the object of special investigations by Whitaker and others (Whitaker, 1939).

Tradescantia bracteata.—

The peculiar binary variation pattern of this species has been the object of a special investigation (Anderson and Hubricht, 1938). The species is a diploid. Chromosome numbers were determined of 40 plants from 25 localities. Two plants from Lawrence, Kansas, were tetraploids and two from Grinnell, Iowa, were

triploids; all the rest were regular diploids. I have suggested (Anderson and Hubricht, 1938) that under the prairie and plains conditions where this species is native, ploidy, with its tendency to increase length of blooming season, would be at a selective disadvantage. The plants from Grinnell and Lawrence show that polyploid strains can arise in this species. The Michigan collection has been checked and represents a truly disjunct distribution, something which is rather rare in these *Tradescantias*. The record from Indiana in Anderson and Woodson was a depauperate specimen of *T. virginiana*.



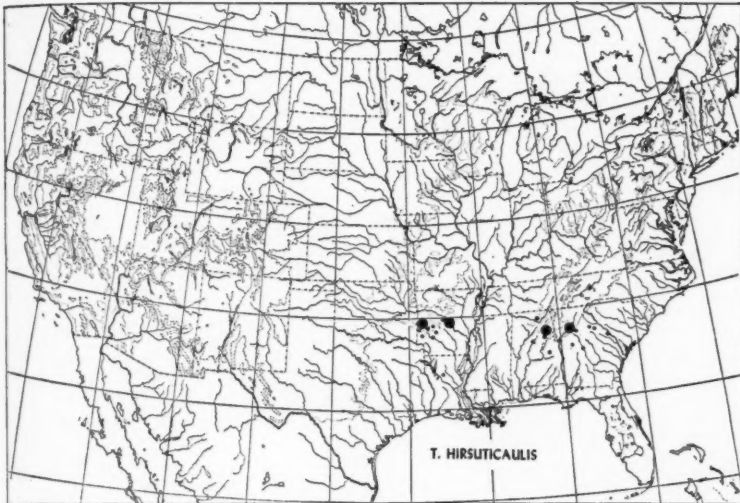
Map 12

Tradescantia birsuticaulis.—

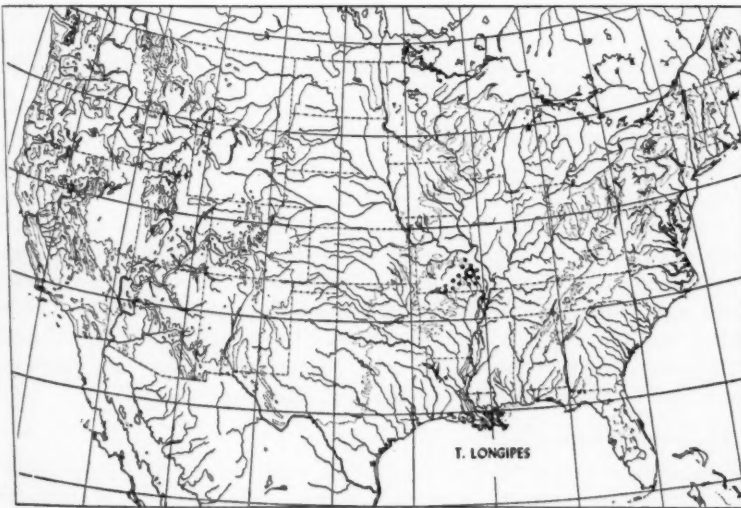
This species is exclusively diploid. Twenty-one plants were examined from ten localities. At two localities plants were found with an extra pair of chromosomes. There were also chromosome fragments in these two plants. One plant from still another locality had very small fragment chromosomes in addition to the diploid complement. These three abnormal plants were from Stone Mountain, Georgia, eastern Arkansas and western Arkansas.

Tradescantia longipes.—

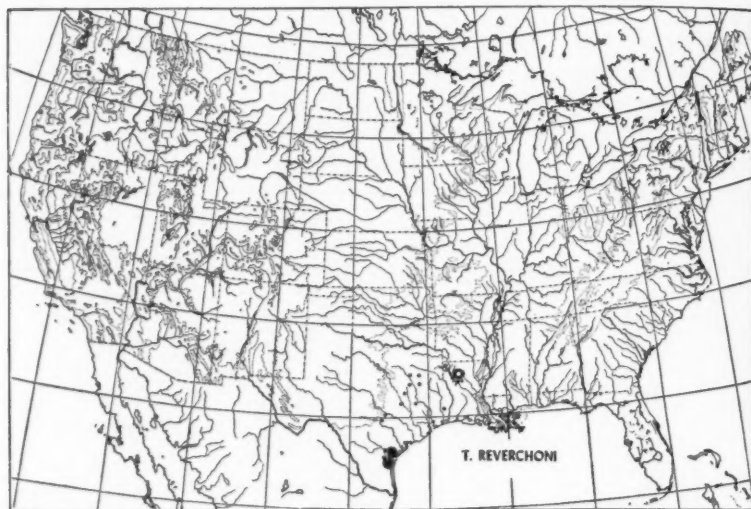
I have three counts on this species from three different localities in Missouri. All three were regular tetraploids. Further collecting has extended the distribution to St. James County, Missouri, on the same general type of soil.



Map 13



Map 14



Map 15

Tradescantia reverchonii.—

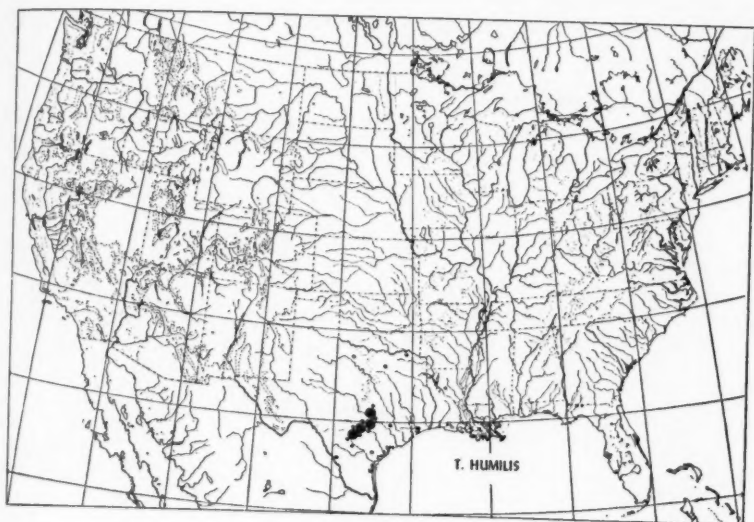
This species is found along the Carizo sand ridge in Texas and on coastal sands. When these sandy soils are brought under cultivation for truck crops, as near Winter Haven, Texas, *T. reverchonii* may hybridize extensively with *T. occidentalis*. We have counts on five plants from two localities in Texas; all were regular diploids. One plant was counted in northwestern Louisiana; it was a regular tetraploid.

Tradescantia humilis.—

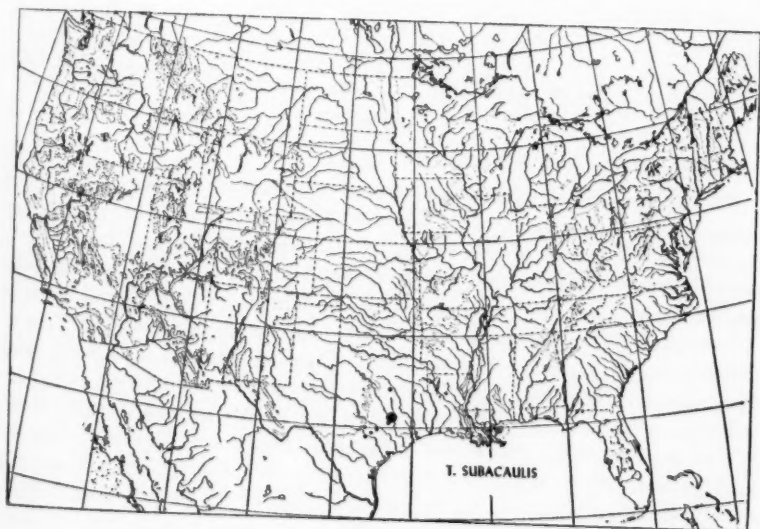
This species was native to the rich black soil at the edge of the coastal plain in Texas and was so common and so conspicuous as to have been collected frequently by early naturalists. Virtually all this land is now in cultivation (much of it in cotton) or in cities and military camps. *T. humilis* lingers on around the fringes of its former home. I have found it along railroads, in bee yards, along roadsides, behind sign boards, in real-estate developments, and along the fences around military establishments. Most of the specimens I collected showed signs of slight introgression from other species, as might be expected under such conditions. Sixteen plants were counted in seven localities; all were regular diploids.

Tradescantia subacaulis.—

This species was counted in two localities. Both plants were regular diploids. While I knew the species well in the herbarium I had not seen it in the field until I made these two collections. It comes up in deep sand, and much of the stem is subterranean. The plant is also rather more succulent than the other species in the *virginiana* group. When it is dug up out of the sand and dried out in a plant



Map 16

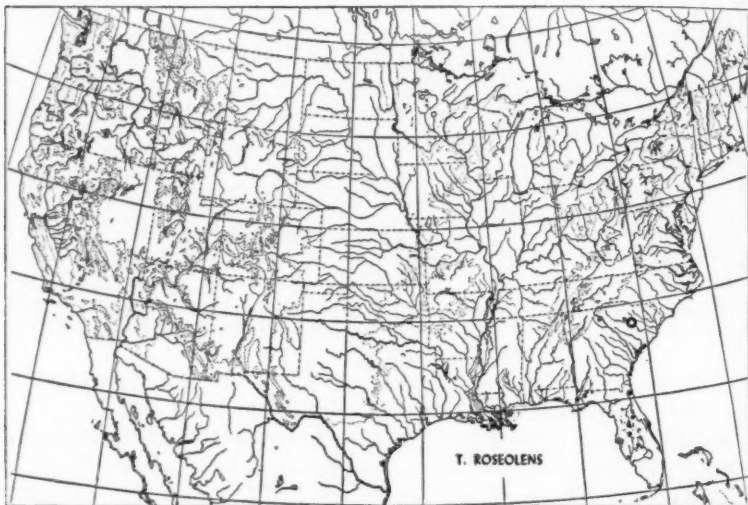


Map 17

press it changes its aspect more radically than any of our other *Tradescantias*. It was therefore not until my specimens were nearly dry that I realized I had at last found *T. subacaulis*.

Tradescantia roseolens.—

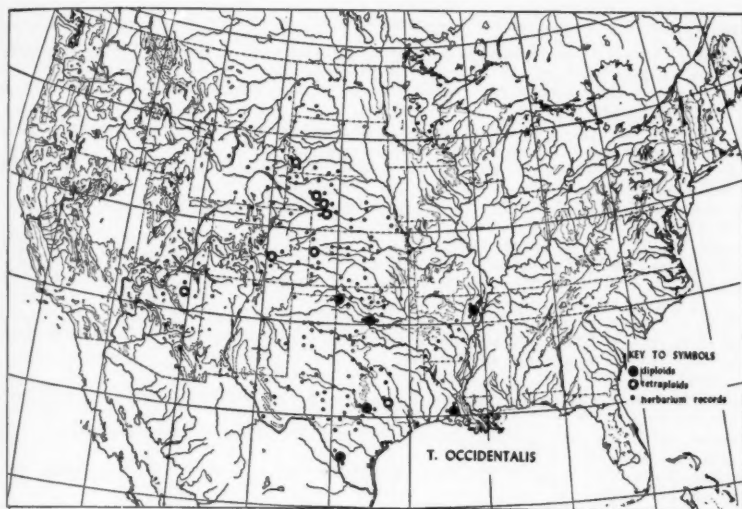
This species was found in the field only once. Five plants were counted; all were regular tetraploids.



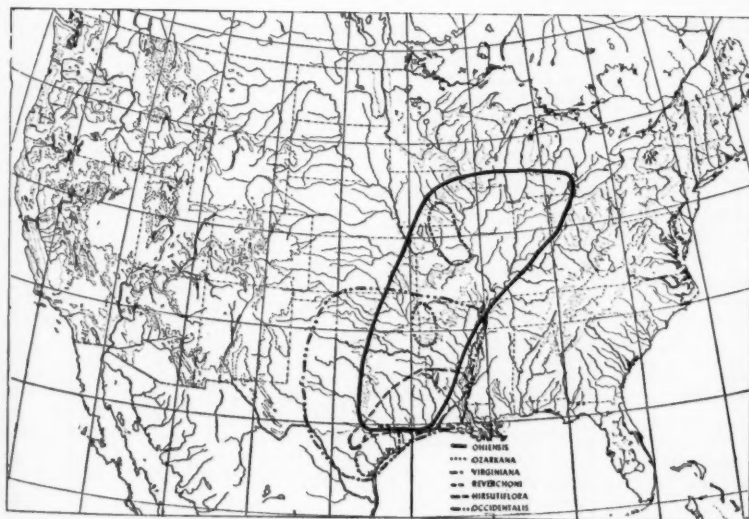
Map 18

Tradescantia occidentalis.—

This species is differentiated both geographically and ecologically. Out of it is coming one of the most aggressive weeds in the Great Plains. Further collecting has extended the record of this species in Louisiana and Arkansas where it is a common plant on sandy terraces which supported natural prairies before they were brought into cultivation. In parts of Texas one can find slender diploid plants of *T. occidentalis* in among the mesquite bushes and coarse tetraploids of *T. occidentalis* along the highway a few feet away. On many a remote mesa in the Great Plains, however, there will be slender little plants, far from any highway, which are tetraploids. Furthermore, the weedy strains are themselves demonstrably differentiated geographically. Part of this, it has been demonstrated elsewhere (Anderson and Hubricht, 1938), is due to extensive introgression from *T. obiensis* which is actively spreading westward far beyond the range of *T. obiensis* itself. Forty chromosome counts were made at 22 localities. At seven localities the 11 plants counted were regular diploids. At 15 localities the 29 plants counted were tetraploids. One of these plants was somewhat irregular with many univalents, and with micronuclei in the microspore. The other 28 were regular.



Map 19



Map 20

Diploid areas of species which are elsewhere tetraploid. It will be noted that these areas tend to center upon Texas as do most of the purely diploid species.

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Plant Name	Locality	2n	4n	2n +2	4n +2
Anderson & Sax (1936)					
<i>T. subaspera</i> var. <i>typica</i>					
	Florida, Torreya State Park		2		
Mordock	Illinois, north of Valmeyer, Monroe Co.		1		
Hazleton	Indiana, Hazleton		1		
New Harmony	Indiana, New Harmony, Posey Co.		1		
Turkey Run	Indiana, Turkey Run		3		
Louisville	Kentucky, Louisville		1		
Smith's Mill	Kentucky, Smith's Mill		1		
Ashland	Missouri, Ashland, Boone Co.		1		
Fertile	Missouri, Fertile, Washington Co.		1		
Hermann	Missouri, Hermann		1		
Marthasville	Missouri, Marthasville		3		
Wolf Creek	Tennessee, near Wolf Creek	1			
<i>T. subaspera</i> var. <i>montana</i>					
Anniston	Alabama, Anniston		1		
Gravel Pit	Alabama, Jacksonville		3		
Hair	Alabama, Jacksonville		3		
Balsam Gap	North Carolina, Balsam Gap		8		1
Cherokee	North Carolina, Cherokee		1		
Mt. Mitchell	North Carolina, Mt. Mitchell		5		
Sylva	North Carolina, Sylva		1		
Knoxville	Tennessee, Knoxville		2		
<i>T. edwardsiana</i>					
Edwardsiana	Texas, near Austin	15			
Bull Creek	Texas, Bull Creek	2			
<i>T. ozarkana</i>					
	Arkansas, Deer		1		
Boston Mtns.	Arkansas, south of Jasper, Newton Co.		1		
Heinze	Arkansas, Rich Mountain, Polk Co.	1			
Hotel	Arkansas, Rich Mountain, Polk Co.	3			
Roaring River	Missouri, Roaring River State Park, Barry Co.		1		

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
<i>T. ernestiana</i>					
	Arkansas, Rich Mountain, Polk Co.	1			
Eagle Rock	Missouri, Eagle Rock, Barry Co.	1			
Jasper	Missouri, Jasper Co.	1			
Elk River	Missouri, Noel, McDonald Co.	2			
Julian	Missouri, Richville, Douglas Co.	4			
<i>T. virginiana</i>					
New Athens	Illinois, 1 mi. west of New Athens, St. Clair Co.	3			
Tobacco Landing	Indiana, Harrison Co.		1		
Portland	Indiana, Portland		1		
H.S.C.	Iowa, Skunk River, Poweshiek Co.	3			
Skunk River	Iowa, bluffs along N. Skunk River, north of Sharon, Poweshiek Co.	2			
Algoving	Missouri, Algonquin Sta., Webster Groves, St. Louis Co.		1		
Fowler Creek	Missouri, east of Ashland, Boone Co.	1			
DeSoto	Missouri, DeSoto, Jefferson Co.				1
Dry Fork	Missouri, Dry Fork	1			
	Missouri, 7 mi. south of Fredericktown, Madison Co.		2		
	Missouri, Goldman, Jefferson Co.		2		
	Missouri, ½ mi. east of Greenville, Wayne Co.		3		
Koester	Missouri, Koester, St. Francois Co.		1		
New Florence	Missouri, New Florence, Montgomery Co.	1			
New Melle	Missouri, New Melle, St. Charles Co.	1			
Mineola	Missouri, Mineola	1			
Cherbonnier	Missouri, 5 mi. west of St. Charles	1			
Selma	Missouri, Selma, Jefferson Co.		1		
Mattese	Missouri, Mattese, St. Louis Co.		1		
Vera	Missouri, Vera, Pike Co.	4			
Peterson	Missouri, Warrenton	1			
Swarthmore	Pennsylvania, Swarthmore		2		
Fort Valley	Virginia, Fort Valley		1		
<i>T. hirsutiflora</i>					
	Arkansas, northeast of Little Rock, Pulaski Co.		1		
Perry	Georgia, Athens		1		
Dorsut	Louisiana, Caddo Parish	1		1	
	Louisiana, Iowa	5			
	Louisiana, L.S.U., Natchitoches, Natchitoches Parish		1		
	Louisiana, Mooringsport Road, Shreveport	2			
	Louisiana, between Scott and Duson		2		
	Texas, west of China	1			
	Texas, 14 mi. south of College Station, Brazos Co.	2			
Corer Lane	Texas, Corer Lane, Wilson Co.	2			
	Texas, between Fairbanks and Cypress	1		1	
	Texas, Gutz Clay Pit Road	1			
Flory	Texas, Hearne, Robertson Co.	1			
Ledbetter	Texas, 1 mi. east of Ledbetter, Fayette Co.	1			
	Texas, east of Liberty	1			
Sutherland Springs	Texas, Sutherland Springs	2			
<i>T. tharpjii</i>					
	Kansas, Miltonvale, Cloud Co.		1		
Rocky Prairie	Missouri, Webb City, Jasper Co.		1		
Scullin	Oklahoma, Scullin		5		

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
<i>T. gigantea</i>					
Cliff Springs	Texas, Austin	18			
Lake Cliff	Texas, Austin	1			
Mo. Pac.	Texas, Austin	8		1	
Onion Creek	Texas, Austin	7			
River Cliff	Texas, Austin	2			
River Terrace	Texas, Austin	5			
Shoal Creek	Texas, Austin	7			
Terrace	Texas, Austin	12			
Bear Mtn.	Texas, Bear Mountain, Gillespie Co.	2			
Buda	Texas, Buda	1			
	Texas, bank of Guadalupe River, Gruene, Comal Co.	1			
Hunter	Texas, Hunter	1			
Mt. Bonnell	Texas, Mt. Bonnell	5			
<i>T. obiensis</i>					
	Arkansas, Kings Canyon, Clarksville		5		1
	Arkansas, Y-City, Scott Co.		1		
Orlando	Florida, Orlando		1		1
Borglum	Georgia, Stone Mountain		1		
Warrenton	Georgia, Warrenton		1		
Warrenton	Georgia, Warrenton		1		
	Illinois, Bellflower, McLean Co.		2		
Pana	Illinois, Pana		1		
	Illinois, Roberts, Ford Co.		2		
Starved Rock	Illinois, Starved Rock, LaSalle Co.		1		
Ullin	Illinois, Ullin		1		
Diamond Lake	Indiana, Diamond Lake, Noble Co.	2			
	Indiana, Indiana Dune State Park		4		
Waterloo	Iowa, Waterloo	1			
	Kansas, Belvue, Pottawatomie Co.		5		
	Kansas, Belvue		2		
	Kentucky, Bardwell	1			
Dorcan	Louisiana, Caddo Parish	1			
	Louisiana, near Saline		2		
	Louisiana, near Shreveport	1			
Steere	Michigan, Ann Arbor	2			
	Michigan, Cedar Springs, Kent Co.		1		
	Michigan, Dexter	5			
Dexter	Michigan, Dexter	1			
Old Mill	Michigan, Grass Lake, Jackson Co.		1		
	Michigan, Homer, Calhoun Co.		1		
	Michigan, Litchfield, Hillsdale Co.		1		
Schoolcraft	Michigan, Portage, Kalamazoo Co.		1		
Reita	Michigan, Schoolcraft	1			
3 Rivers	Michigan, Three Rivers	1			
	Minnesota, Peterson		1		
McKee	Mississippi, State College		6		1
Algonquin	Missouri, Algonquin Sta., Webster Groves, St. Louis Co.		6		
Antonia	Missouri, Antonia, Jefferson Co.		2		
	Missouri, east of Brookfield, Linn Co.		1		
	Missouri, 3 mi. north of Drake, Gasconade Co.		1		
Florissant	Missouri, Florissant, St. Louis Co.		1		
Hamburg	Missouri, Hamburg		4		
La Barque	Missouri, La Barque Creek		1		
Red Rock	Missouri, Red Rock, Hughes Mountain		1		
Royal Gorge	Missouri, Royal Gorge, Iron Co.		1		

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
Wash. U.	Missouri, St. Louis		2		
Berry	Missouri, Warrensburg, Johnson Co.		2		
South Webster	Missouri, Webster Groves, St. Louis Co.		1		
Bolton	North Carolina, Bolton		3		
	Oklahoma, Hughes		1		
Platt Nat. Park	Oklahoma, Platt National Park, Murray Co.		1		
Turner Falls	Oklahoma, Turner Falls, Murray Co.		1		
Reflexa	Texas, Austin	1			
	Texas, Hearne	1			
Keller	Texas, Keller	2			
	Texas, between Pine Island and China	2			
	Virginia, Eagle Rock		1		
Mountain Lake	Virginia, Mountain Lake, Giles Co.		1		
Madison	Wisconsin, Arena		1		
Baraboo	Wisconsin, Baraboo		2		
	Wisconsin, 6 mi. northwest of Baraboo, Sauk Co.		2		
	Wisconsin, 3 mi. northwest of Big Spring, Adams Co.		1		
	Wisconsin, 2 mi. southwest of Caloma, Waushara Co.		1		
	Wisconsin, 3 mi. east of Friendship, Adams Co.		2		
Jolivet	Wisconsin, La Crosse		2		
	Wisconsin, Nekeosa, southeast corner Wood Co.		1		
	Wisconsin, Plainfield Lake, Waushara Co.		2		
	Wisconsin, Spring Green		1		
Tomah	Wisconsin, Tomah		1		
	Wisconsin, Viroqua		1		
	Wisconsin, 3 mi. south of Wisconsin Dells, Adams Co.		2		
	Wisconsin, 9 mi. north of Wisconsin Dells, Adams Co.		2		
<i>T. paludosa</i>					
Acadosa	Louisiana, Acadia Parish	1			
Brown	Louisiana, Baton Rouge	1			
	Louisiana, Bennettsville, Rapides Parish	1			
Gentilly	Louisiana, Gentilly	13			
<i>T. bracteata</i>					
Clarke	Iowa, Grinnell	1			
Grinnell	Iowa, Grinnell	2			
Harris Grove	Iowa, 4 mi. north of Grinnell, Poweshiek Co.	2			
Kellogg	Iowa, Kellogg, Jasper Co.	1			
Kendallville	Iowa, Kendallville, Winneshiek Co.	1			
Pierson	Iowa, Pierson, Woodbury Co.	1			
Tama	Iowa, Tama	3			
Victor	Iowa, 1 mi. west of Victor, Poweshiek Co.	1			
	Kansas, Lawrence		2		
Gates	Kansas, Manhattan	2			
Manhattan	Kansas, Manhattan	1			
Rock	Minnesota, Beaver Creek, Rock Co.	1			
Preston	Minnesota, Preston, Fillmore Co.	1			
Worthington	Minnesota, Worthington	1			
Chain of Rocks	Missouri, Chain of Rocks, St. Louis Co.	1			
Portage des Sioux	Missouri, Portage des Sioux, St. Charles Co.	8			
Overton	Nebraska, Overton, Dawson Co.	3			
Royal	Nebraska, Royal	1			
Huron	South Dakota, Huron, Beadle Co.	1			
Kennebec	South Dakota, Kennebec	1			
Murdo	South Dakota, Murdo	1			
Rockerville	South Dakota, Rockerville, Pennington Co.	1			
Wasta	South Dakota, Wasta, Pennington Co.	2			
S. Dakota	South Dakota, Wind Cave, Custer Co.	1			
Houlton	Wisconsin, Houlton, St. Croix Co.	1			

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
<i>T. hirsuticaulis</i>					
Jacksonville	Alabama, Jacksonville	2			
Showal	Alabama, Jacksonville	1			
Quad Petal	Alabama, Whites Gap	1			
Whites Gap	Alabama, Whites Gap	1			
	Arkansas, northeast of Little Rock, Pulaski Co.	5			
Montgomery	Arkansas, Montgomery Co.	6			
Y-City	Arkansas, Y-City, Scott Co.	2		1	
North Slope	Georgia, Stone Mountain	1		1	
<i>T. longipes</i>					
Killarney	Missouri, Lake Killarney, Iron Co.		1		
	Missouri, Old Silver Mine, Madison Co.		1		
Spring Creek	Missouri, 5 mi. north of Stanton, Franklin Co.		1		
<i>T. reverchoni</i>					
Lucky	Louisiana, Lucky, Bienville Parish		1		
Flour Bluff	Texas, Flour Bluff	1			
	Texas, Ingleside, near Corpus Christi	4			
<i>T. bnmilis</i>					
Nigger D. & D.	Texas, Austin	3			
	Texas, Lockhart, Caldwell Co.	1			
	Texas, New Braunfels, Comal Co.	2			
	Texas, 10 mi. south of New Braunfels, Comal Co.	1			
Oakhill	Texas, Oakhill Road	7			
	Texas, Saline	1			
	Texas, W. W. White Road, Kyle	1			
<i>T. subacaulis</i>					
	Texas, Bryan, Brazos Co.	1			
	Texas, south of College Station, Brazos Co.	1			
<i>T. roseolens</i>					
Columbia	South Carolina, Columbia		5		
<i>T. occidentalis</i>					
Winslow	Arizona, Winslow		1		
Ellsmere	Colorado, Ellsmere		1		
Manitou	Colorado, Manitou		1		
Somena	Kansas, Somena		1		
	Louisiana, between Scott and Duson	2			
Brady	Nebraska, Brady, Lincoln Co.		1		
Chadron	Nebraska, Chadron, Dawes Co.		1		
Tryon	Nebraska, Tryon		1		
	Nebraska, Tryon, McPherson Co.		1		
	Nebraska, Whitman, Grant Co.		2		
Belew	Oklahoma, Harmon	1			
	Oklahoma, Indian Springs, south of Norman	1			
Paoli	Oklahoma, Paoli	1			
Horsechief Lake	South Dakota, Horsechief Lake		1		
S. Dakota	South Dakota, Wind Cave, Black Hills		1		
Austin	Texas, Austin	4			
Ilex Grove	Texas, College Station		8		
Jeanette	Texas, College Station		3		
Mangelsdorf	Texas, College Station		4		
Signal	Texas, College Station		2		
	Texas, 14 mi. south of College Station	1			
	Texas, Miranda, Webb Co.	1			

Species of <i>Tradescantia</i>	2n		4n		2n + 2		4n + 2	
	Populations	Individuals examined	Populations	Individuals examined	Populations	Individuals examined	Populations	Individuals examined
<i>sabaspera typica</i>	1	1	11	16
<i>sabaspera montana</i>	8	24	1	1
<i>edwardsiana</i>	2	17
<i>osarkana</i>	2	4	3	3
<i>ernestiana</i>	5	9
<i>virginiana</i>	11	19	11	16	1	1
<i>hirsutiflora</i>	12	20	4	5	2	2
<i>tbarpii</i>	3	7
<i>gigantea</i>	13	70	1	1
<i>obiensis</i>	12	20	56	96	3	3
<i>paludosa</i>	4	16
<i>bracteata</i>	24	39	1	2
<i>hirsuticaulis</i>	8	19	2	2
<i>longipes</i>	3	3
<i>reverchonii</i>	2	5	1	1
<i>humilis</i>	7	16
<i>subacaulis</i>	2	2
<i>roseolens</i>	1	5
<i>occidentalis</i>	7	11	15	29
	112	268	117	207	5	5	5	5

Total populations studied 230
 Total individuals examined 485



INTROGRESSION OF *SALVIA APIANA* AND *SALVIA MELLIFERA*

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AND BURTON R. ANDERSON

Salvia apiana and *Salvia mellifera* are two common species of sage in coastal California. Over much of their overlapping ranges they give little or no indication that they can (and frequently do) hybridize and that their hybrids are quite fertile. These significant facts were called to scientific attention by Epling. After monographing these and other *Salvias* taxonomically (Epling, 1938), he studied them experimentally in the field and in the breeding plot. He demonstrated (Epling, 1947) that they hybridize readily when artificially cross-pollinated and that the resulting hybrids are fertile enough to yield variable F-2's and back-crosses. Though these two species grow closely intermingled over thousands of square miles he found little evidence that hybridization did take place except under disturbed conditions. This he interpreted as due to a complex of internal and external barriers. One of the most important is the different adaptive mechanisms for insect pollination in the two species, *S. apiana* being pollinated largely by bumble bees and *S. mellifera* by small solitary bees.

The problem seemed such an interesting one that the senior author has studied it repeatedly and intensively in the field for somewhat over a decade and has used these two species as field and laboratory material for a summer school course. Population samples from critical areas were pickled for laboratory study, and with the help of the junior author an exhaustive analysis of variation in pubescence, calyx shape, corolla shape, and inflorescence branching was undertaken. This confirms and extends Epling's experimental and field studies. It analyzes a little more precisely the conditions under which the barriers break down between the two species. Thanks are due to Carl Epling, to Harlan Lewis, and to E. G. Anderson for assistance in making the collections.

In addition to the various facts collected by Epling, careful study of two quite different matters seemed necessary before we could interpret the hybridization dynamics of these two species: (1) a more complete morphological analysis of the two species and their intermediates; (2) a precise investigation of the disturbed habitats in which intermediates were common.

MORPHOLOGICAL ANALYSIS OF SPECIES DIFFERENCES

If one is effectively to analyze the variation pattern in populations where hybridization is known or suspected, the first *desideratum* is a thorough understanding of the nature of the differences between the hybridizing entities. *Salvia apiana* and *Salvia mellifera* are well-differentiated species, distinguishable at a glance, but if we are to use this difference as a yardstick in measuring what is happening in populations, we must refine our understanding of it to the point where we can distinguish *S. mellifera* with eight ancestors out of eight belonging to

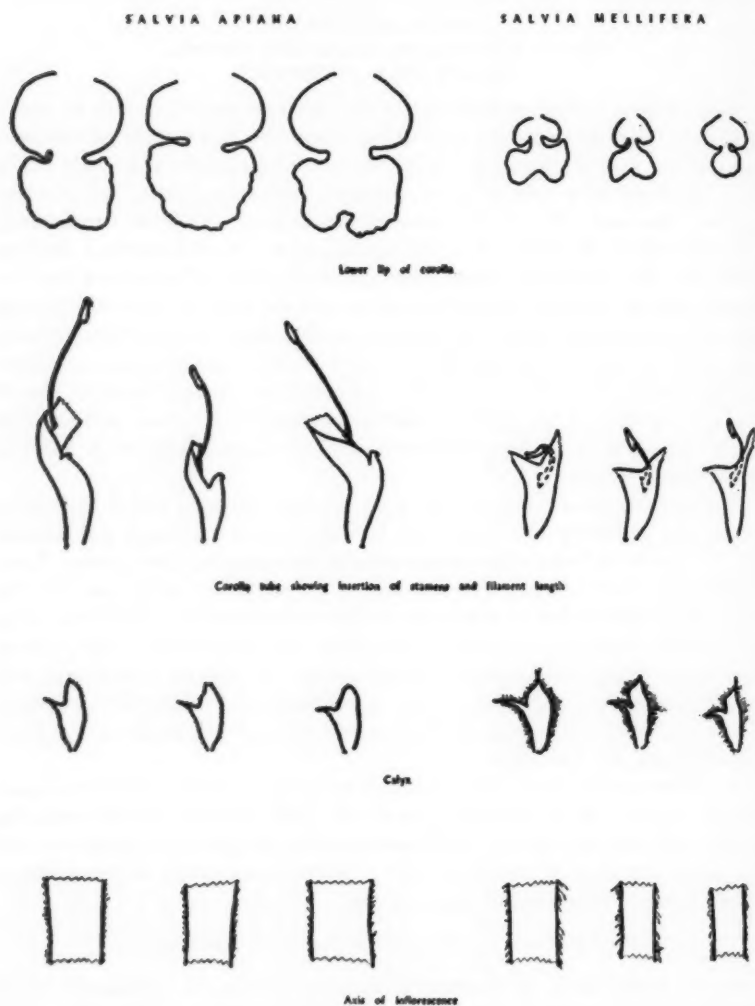


Fig. 1. Drawings of portions of *Salvia* flowers used in analyzing variation pattern. Comparable portions of three plants of *Salvia apiana* and three of *Salvia mellifera* were drawn to scale with camera lucida. Upper row ($\times 2$); second row ($\times 2$) showing filament lengths and position of stamen insertion in corolla tube; third row, calyx ($\times 2$), showing length of terminal spine and length of pubescence; bottom row ($\times 8$), view from the side showing length and direction of pubescence.

INTERMEDIATE

SUB-MELLIFERA



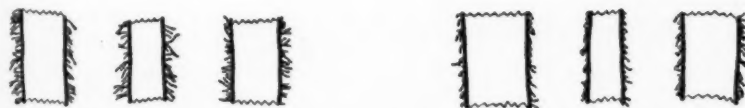
Lower lip of corolla



Corolla tube showing insertion of stamens and filament length



Calyx



Axis of inflorescence

Fig. 2. Camera lucida drawings of three hybrids and three plants of probable hybrid ancestry from the "Olives" population; same scale and same portions of the flower as in fig. 1. Note the intermediacy of the plants at the left compared to those in fig. 1. The plants to the right, when compared with the examples of *S. mellifera*, are typical of the variation pattern produced by introgression. Note that though all three are similar to normal *S. mellifera*, they are more variable, and their slight departures from the average are mostly in the direction of *S. apiana*.

that species, from a second back-cross seven of whose ancestors came from it and one from *S. apiana*. Species (and subspecies) characteristically differ in many ways; a species difference seen as a whole is compounded of many things (Anderson, 1954). Differences in proportion are more common than differences in absolute size, while differences in change of proportion with size are even more characteristic. Pubescence *patterns* are as important as pubescence and color *patterns* are as important as differences in color. One needs to define in as exact terms as possible the totality of this difference so that it can be used with precision in population analysis. There are other *Salvias* in southern California besides *S. apiana* and *S. mellifera*; we need to understand the difference between *S. apiana* and *S. mellifera* so thoroughly that we can unhesitatingly distinguish between introgression of these two species and introgression of either of them with *S. clevelandii*, for instance. To do this job well requires repeated and exhaustive examination. The differences do not come with labels on them; as Linnaeus said long ago, "The characters are where you find them." A slipshod examination of the differences can produce nothing better than a slipshod interpretation of the population dynamics.

The characters eventually used (see fig. 1) were as follows:

(a) *The length of the lower lip of the corolla, measured to the nearest millimeter.*—This is precisely the character used by Epling.

(b) *Point of insertion of the stamens.*—In *S. mellifera* the stamens are inserted on the corolla well inside the tube; in *S. apiana* well outside. This character was scored in the following grades: well inside tube, barely in or barely out, well outside tube.

(c) *Pubescence of calyx.*—*Salvia mellifera* has coarse hairs on the calyx, particularly along the veins. The pubescence of *S. apiana* is so short and dense that it does not look like hairs at all, except under high magnification. The length of the longest hairs on the calyx was measured to the nearest millimeter.

(d) *Length of terminal spines on calyx.*—The calyx lobes of *S. mellifera* are tipped with long weak spines; in *S. apiana* the spines are so short as to be virtually invisible. This character was scored by measuring the spines at the tip of the upper lobes to the nearest millimeter.

(e) *Pubescence on the axis.*—Both *S. apiana* and *S. mellifera* have appressed pubescence on the axis of the inflorescence. In *S. mellifera* the hairs are pointed downwards; in *S. apiana* they point upwards. They were scored in the following grades: downward, outward, upward.

(f) *Length of filament,* measured to nearest millimeter.

FIELD STUDY

Hybridization between the two species was studied on the lower slopes of the San Gabriel Mountains above Arcadia, California. This site was originally chosen not for any special features but because (for the laboratory where the senior author was working) it was the closest spot at which the two *Salvias* could be found in profusion. They were studied mainly along a footpath which wound westwards

(more or less on the contour) from the road up the Santa Anita Canyon. Less intensive field studies were carried on at several other locations. In this area the slope of the mountains is prevailing toward the south. It is so steep as to approximate the pitch of a church roof, and the thin soil is stony with rock particles. As reported by Epling, though the two species frequently grow intermingled, *Salvia apiana* showed a preference for the drier sites. Along the steepest and jutting ridges, it grew in almost pure stands, while in shadier and moister spots along sections of the trail only *Salvia mellifera* was represented. The trail is one much used for recreational purposes and the vegetation along it has suffered repeated incursions from the public. Beer cans dot the landscape, particularly near the road. Half-formed side-trails are common, and the shrubs and larger perennials bear the scars of repeated vandalism. The site had been subject to disturbances for some decades, yet the flora as a whole was largely native. Out-and-out weeds were rare and the *Salvias* (at first glance) did not seem to have mongrelized at all. There were no apparent hybrids, and the casual impression was that for these two species one had nothing except typical specimens of *Salvia mellifera* and of *Salvia apiana*. The latter species, to be sure, is extremely variable, but the variations all tend in the direction of *Salvia apiana* var. *compacta* (see below) and seemingly have nothing to do with *S. mellifera*.

Closer plant-by-plant inspection did not quite bear out this conclusion. In one of the gullies, close to the point at which the path left the road, the vegetation bore the scars of intensive vandalism. Here there were a number of plants of *S. mellifera* which varied more from plant to plant than is typical for this species. Careful examination demonstrates (see below) that this variation (in so far as it is measurable) is all in the direction of *S. apiana* and presumably represents slight introgression from that species. A meticulous examination of every plant along the path indicated that introgression from *S. apiana*, so slight as scarcely to be apparent even to the experienced eye, had taken place at several points along the trail.

At one point, however, there had been much introgression, and this area was studied intensively. There were a few plants obviously intermediate between the two species, and others which were more or less like *S. apiana* or like *S. mellifera* but with color patterns, growth habits, corolla shapes, and inflorescences which were clearly atypical. It was not until the area had been repeatedly visited that it became evident that the hybrids and introgressants formed a compact population confined to a distinct area, only one corner of which abutted on the trail.

Even from the first examination it was evident that this area was at the point where the trail came down the farthest from the mountain side, to a spot once occupied by oaks. Gradually it was realized that the variants were confined to a space where some years ago the oaks had been cut and a small grove of olives had been planted. The olives had been abandoned but had continued to grow, and native vegetation had spread in around them. The upper corner of this area, which was crossed by the trail, had been used repeatedly for camping and some of the

trees had been cut. It was in this doubly disturbed spot that most of the strangest-looking hybrids were found, but the entire area in among the abandoned olives, in so far as it had any *Salvias*, had nothing but atypical ones. Some of them were so grossly atypical as to be readily demonstrable as such in the pictorialized diagram (fig. 3) which takes account of only six measured characters. Some were so similar to *Salvia mellifera* that to demonstrate their introgressive origin would require careful scoring of such evanescent characters as flower color pattern and the angles at which the stamens are held.

ANALYSIS OF VARIATION

Collections were made from every plant abutting on the trail and from the area in among the olives. These were treated as two population samples, "path" and "olives." The data are presented as pictorialized scatter diagrams and as frequency distributions for a hybrid index based on these diagrams in figs. 3 and 4. Drawings to scale are shown in figs. 1 and 2 for a few representative plants. It will be seen that the population along the path is mostly composed of plants of the two species which show little or no indication of introgression but that a few of the *S. mellifera* showed slight introgression from *S. apiana*, about as much as we would expect in a second back-cross (i.e. in plants with seven ancestors from *S. mellifera* and one from *S. apiana*). The "Olives" population is clearly mongrel. Off-type plants are in the majority. Seen as a whole they represent the kind of criss-crossing recombinations of intermediate characters so typical of hybrid populations whether natural or artificial. In the area of the abandoned olive orchard such mongrels are clearly in the majority; had it been possible to score such characters as color pattern it would probably have been possible to demonstrate that they make up virtually the entire population.

DISCUSSION

This example of introgression between *S. apiana* and *S. mellifera* is in some ways the most illuminating of the numerous examples of hybridization in natural populations which have been reported in recent years. Let us summarize the main points. Two species easily hybridized in the experimental plot do not ordinarily hybridize in the field, though they grow intermingled over wide areas. However, in a strange habitat (or collection of strange habitats) adjacent to their natural range, hybrids and their mongrel descendants press in to the virtual exclusion of the parental species. There are several important inferences which can be drawn from this example. The abundance of hybrids in the field, once a habitat is provided in which they are at an advantage, demonstrates that there is no barrier (as such) to hybridization between these species. Hybrids are virtually absent, not because they are not being produced but because when they do occur there is no place for them. The association of which these two *Salvias* are a part has been through the sieve of natural selection. All kinds of species in it have been continuously selected for getting on with each other; they form a multi-dimensional

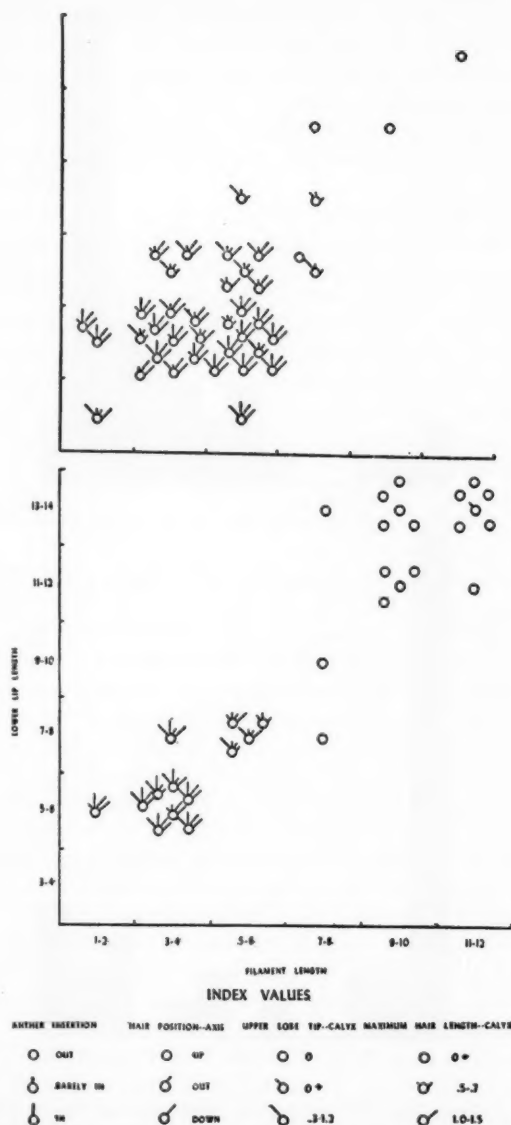


Fig. 3. Pictorialized scatter diagrams of two populations of *Salvia*; above "Olives" population, below "Path" population. Each circle illustrates a single plant. Lengths of filament and of corolla are measured and diagrammed the same in both populations, though indicated only in the lower example.

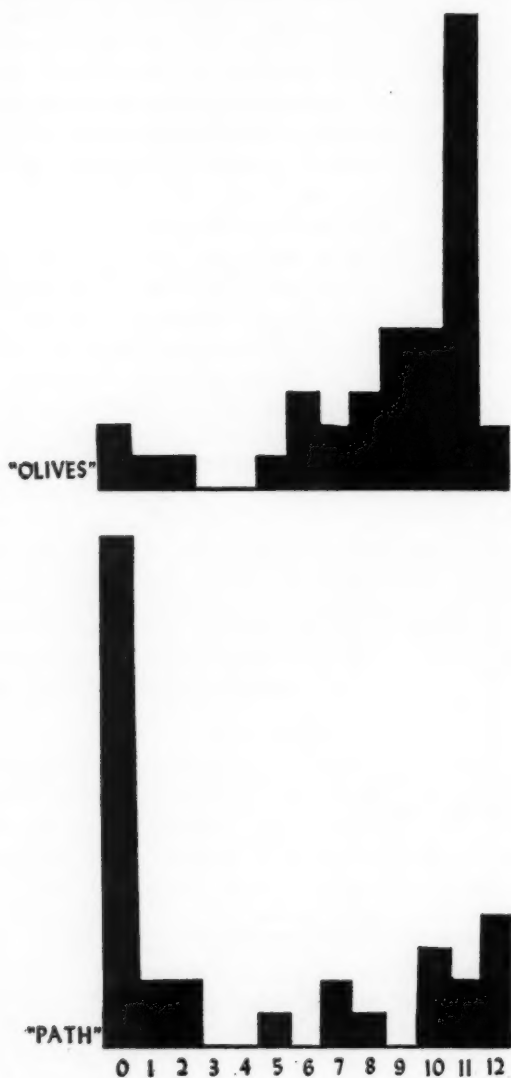


Fig. 4. The data of fig. 3, diagrammed as frequency distributions on a hybrid index which has values running from 0 for "*good*" *mellifera* to 12 for "*good*" *apiana*. Further explanation in the text.

jig-saw puzzle the pieces of which fit tightly together. There is no place in this closed association for an intermediate between any two species, or even for minor variants. It is not until a new ecological dominant, like man (Sauer, 1952), comes along and makes a set of radically new habitats that the hybrids can even demonstrate their presence readily. When this happens not only can they grow and persist but among their mongrel and variable descendants are various new recombinations, some of which are at a selective advantage in the relatively open associations produced by man.

By reference to only two of the most obvious physical variables, soil and sunshine, one can demonstrate what radically new habitats are presented by the olive orchard. Previously there had been dry sunny hillsides with pockets of soil, and shady oak woods with black woods soil. Cutting down the oaks and planting the olives produced pockets of sun, shade, and semi-shade on top of black woods soil. Planting out olives introduced an alien tree which, however, had been selected for such Mediterranean climates. On the other hand, the young trees were spaced out away from each other and from woody vegetation in a way quite unlike anything in the native woody flora. It was in these highly peculiar habitats that the variable progeny of the original hybrids had been at a selective advantage. Though we have no proof of the assumption, it seems likely that the hybrid progeny growing there are but a small and highly selected representation of the offspring originally seeded into the area.

It was Darlington (1939) who first pointed out clearly that the short-range and long-range effects of natural selection are almost diametrically opposed and that evolutionary systems which manage somehow to meet both these needs tend to be favored. The immediate need of the next generation is to conserve the adaptation already achieved. In a mature association this means producing offspring as much like the successful parent as possible. In such an association any surviving organism has fitted well into a particular niche; its offspring to succeed as well should have the same characteristics. The long-time need of the species, however, is for enough variability so that when changes arise in the physical and biological environment, the species is at length able to fit into a new niche, or even into new niches. Darlington pointed out how the side-by-side operation of apomictic and sexual reproductive systems in various plant genera allowed the successful individuals to produce, apomictically, offspring which were exact copies of the successful parent, though still retaining the capacity (by sexual reproduction) to produce variable descendants some few of which might be at a selective advantage in a changed or changing environment.

As more and more cases of introgressive hybridization have been analyzed, it has become increasingly clear that such genera as *Salvia* provide an almost ideal solution for this seemingly insoluble dilemma. It has been demonstrated repeatedly (and with increasing clarity) that hybrids and back-crosses are rare in natural populations not because of strong sexual barriers but because in mature associations

of plants and animals which have evolved in each other's presence the whole association is closed. It is a complex interlocking system of mutually accommodating niches. Hybrids and back-crosses are absent not because they cannot arise but because when they do there is no place for them. Let man arrive and throw the whole association out of balance; let mammalian herbivores (as in New Zealand) be unleashed upon a vegetation with no previous experience of such beasts, and mongrel populations press into the new niches which have been created and themselves take part in building up a new interlocking system. Those genera, therefore, are at an over-all selective advantage which can build up complex barrier systems of exterior agents (in the wide sense) that protect the successful adaption from change so long as the association of which it is a part goes along its old ways, and yet can spawn hybrids and back-crosses in direct proportion to the breaking up of the old association. Genera with very strong internal barriers (such as complete hybrid sterility between well-differentiated taxa) would eventually perish under such changes and doubtless have.

SUMMARY

1. Introgression between *Salvia apiana* and *Salvia mellifera* (previously studied in the field and in the breeding plot by Epling) was studied intensively in the San Gabriel Mountains.
2. As previously noted by Epling, the two species, though highly interfertile, intergrade only slightly or not at all, even when growing intermingled over very wide areas.
3. Extensive introgression was discovered in a small localized area. It proved to be an abortive olive orchard established some years ago among live oaks adjacent to the mountain side where the *Salvias* were native. Among these olive trees hybrids and back-crosses between these two species grew in abundance and even formed the bulk of the population.
4. The evolutionary significance of these facts is briefly discussed.

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INTROGRESSION IN ADENOSTOMA

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On any theory of evolution, differences between individuals are compounded somehow into specific and eventually into generic differences. An efficient analysis of plant-to-plant variation should give us critical data for determining the origin of the basic variability which is the raw material for evolution. If, as is currently generally believed, this basic variability results from gene mutation, then an efficient analysis of individual-to-individual differences should reveal the kind of local differentiation pattern which might be explained on such an hypothesis.

For such studies *Adenostoma fasciculatum*, the common "chamise" of coastal California, is excellent material. Over a large part of its range, plant-to-plant variation is so conspicuous as to compel attention. In the hills behind Palo Alto or on the burned-over slopes of Mt. Diablo, virtually any three or four plants of *Adenostoma* chosen at random can be used to demonstrate the magnitude of this variation and its strongly germinal basis (figs. 1 and 2).

If we examine adjacent bushes of *Adenostoma* along a mountain pathway, it is easy to show that though they are growing so closely side by side that their branches interlock, we can readily distinguish the branches of any one bush by the general similarity of their inflorescences. Though parts of some bushes may be in the sun and parts in the shade, though some branches may be strong terminal leaders and others physiologically suppressed, all the branches on any bush have a "nucleus of common features," while the differences from one plant to another are always perceptible and are frequently conspicuous. If we choose a few good-sized bushes and remove the terminal inflorescences from each four to five well-developed branches from each and lay them in the pathway, an independent observer can easily determine from exactly which bush in the vicinity each set of branches was collected. By actual experiment it has been determined that under these conditions a class of students can match up a series of branches with a series of bushes without a single error. Any three such *Adenostoma* bushes are as different from each other as are three named varieties of lilacs in a collection in a botanical garden. Like the lilacs, they have a strong tendency for all the trusses of bloom on any one bush to be recognizably similar and yet for the trusses to vary perceptibly (and sometimes conspicuously) from one plant to another. Unlike the lilacs, however, the variation is largely confined to differences in the size and branching pattern of the inflorescence. Frequently this may be the only noticeable difference between adjacent bushes, though occasionally one may also find single plants which differ in height, in length of the leaves, in leaf shape, and (even more rarely) in the scurfiness or pubescence at the base of the calyx. Flower color, flower size, and flower shape are not noticeably different in any of the material.

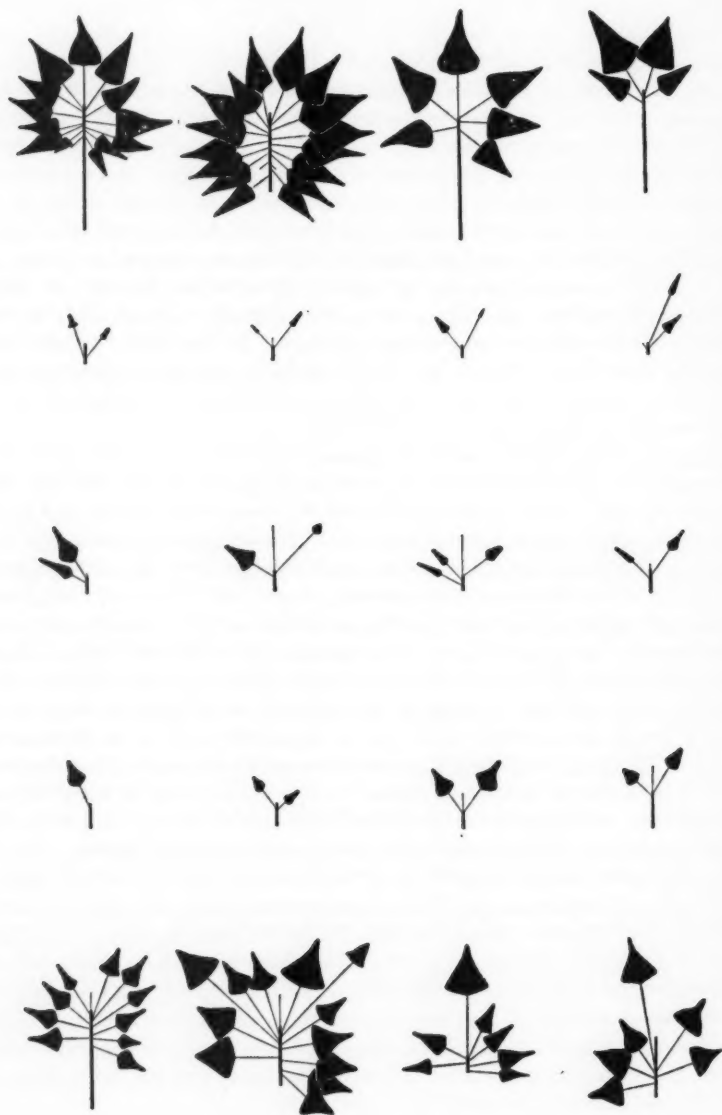


Fig. 1



Fig. 2

Figs. 1 and 2. A comparison of inflorescence differences within plants and between plants in *Adenostoma*. Each drawing is a tracing of an actual specimen, and they are all printed to the same scale (\times approximately .1). The heavy dark line in each separate figure represents the terminal portion of the previous year's growth (primary axis). The thinner lines departing from it are axes of the secondary inflorescences of this season's growth. The triangular to diamond-shaped masses are traces of the outline of ultimate inflorescences.

Fig. 1 (opposite page). Four branches per bush from five different and closely adjacent bushes (each horizontal row represents four different branches from the same bush).

Fig. 2 (above). One branch each from twelve different bushes of *Adenostoma*, printed to the same scale (\times .1) and collected from the same general locality (west of Palo Alto golf course) as the branches illustrated in fig. 1. Note how much difference there is from bush to bush compared to the differences within each bush for such characters as: number of secondary inflorescences; length of peduncle; size and shape of ultimate inflorescences; extent to which terminal inflorescence is or is not differentiated from the other ultimate inflorescences.

A preliminary morphological examination demonstrated that the variability of the inflorescences can be broken down in terms of several quite different elementary variables. Taken all together, they produce at the one extreme a small inflorescence so highly condensed that the separate flowers are tightly packed together into one mass. At the other extreme, a large open panicle is made up of flowers well isolated from one another. The five elementary variables (see fig. 3) producing smaller, denser inflorescences are: (1) shorter internodes, (2) more secondary branches on the primary axis, (3) more flowers from a single node, (4) more telescoped nodes, (5) more branching of the fourth degree at the base of the tertiary branches. The larger, more open panicles, on the contrary, are produced by (1) longer internodes, (2) fewer secondary branches on the primary axis, (3) only one flower per node, (4) no telescoped nodes, (5) no evident branchlets at the base of the tertiary

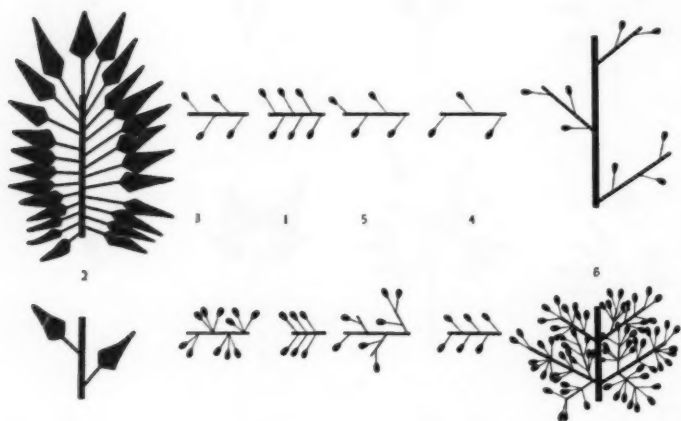


Fig. 3. Diagram showing the various components of inflorescence density in *Adenostoma*. These should be compared with fig. 4 which are tracings from actual inflorescences. The extremes ordinarily met with in the Palo Alto population are shown for each character, though the upper extreme for number of secondary inflorescences on the primary axis is too large for successful illustration and has been omitted. At the extreme left (No. 2) is illustrated the character of number of secondary inflorescences; below, two secondaries, above 25 secondaries. The four different components of density (Nos. 3, 1, 5, and 4) are illustrated from left to right; in each case the open extreme is shown above, the denser, below. No. 3, number of flowers per node; No. 1, number of telescoped internodes; No. 5, amount of branching of the fourth degree; No. 4, length of internode. At the right (No. 6) are shown comparable portions of two inflorescences combining all four factors for density of inflorescence. The diagram above the number 6 shows a small portion of an inflorescence which has simultaneously: only one flower per node; no telescoped nodes; no quaternary branching; long internodes. The one diagrammed below it shows simultaneously: several flowers per node; telescoped nodes; quaternary branching; and short internodes. In No. 6 the erect heavy line represents a portion of the secondary axis and the lines diverging from it are tertiary axes. As in Nos. 3, 1, 5, and 4, each small pear-shaped dot represents a single flower.

branches. These various elementary variables making for more or less density of the inflorescence are illustrated diagrammatically in figs. 3 and 4.

As is demonstrated in fig. 5, these five elementary variables, each in its own way making for a more or less open panicle, can recombine within wide limits. One may have many telescoped internodes with only a single flower at each internode, or one may have three or more flowers at each internode (incipient branching?) without any of the nodes being telescoped. Only when the total population sample is studied is it apparent that *on the average* the shorter internodes, the fewest secondary branches, the largest number of flowers per node, the telescoping of internodes, and the development of branches on the tertiaries all *tend* to occur together.



Fig. 4. Diagrams to scale ($\times .9$) of flower number and arrangement in two actual inflorescences of *Adenostoma*. Though one is more open than the other, neither represents either the extreme of openness or of density realized in the Palo Alto population. The dense extreme, for instance, would look like a solid mass if diagrammed in this manner.

The more clearly one is able to apprehend the variation pattern of all these five variables, the more certain is it that their association is far from random. Let us, for example, consider precisely the chances of finding an individual plant which showed the extreme value for each of these five variables. If we merely consider the upper quarter of the population for any one character the chances of finding a plant which is as extreme as that is, of course, 1 in 4. For any two characters it is $\frac{1}{4} \times \frac{1}{4}$ or 1 in 16. The chances of finding a plant which is in the upper quartile for each of five characters is $(\frac{1}{4})^5$ or 1 in 1024. The chance of finding a single such plant in a collection made from 30 plants is $30/1024$, about 1 in 34, if these characters *were not associated*. Actually three such plants were found in the very first collection, and such multiple extremes have been found in every population sample. When, as will be demonstrated below, the number of measured characters was increased to seven, extreme individuals which measured in the upper fourth of the distribution for each of these seven characters were still met with in every population though the chances of getting such an individual with random association of all seven characters is $(\frac{1}{4})^7$ or less than 1 in 16,000.

These variables were measured as follows:

Number of flowering secondary branches.—

The key to understanding variation in the inflorescences of *Adenostoma* turns on an extremely elementary point. We need to distinguish carefully between growth of the current season and of the previous one. The new growth has a more or less straw-colored surface; that of the previous season has darkened to gray. When attention is paid to this simple point one can readily distinguish comparable portions of the inflorescence. Until that is done he is apt to confuse a whole set of small inflorescences on a plant of the dense extreme with the widely separated branches of a single inflorescence in the opposite, open-flowered type (see fig. 2, for example). In the former there may be only one or two secondary inflorescences departing from the apical portion of any primary stem, while in the latter as many as 30 or 40 secondary branches will depart from the apical portion of each well-developed primary. In making the collections care was taken to choose a primary branch which was typical for the well-developed branches on that particular bush. Since there are ordinarily hundreds of such branches on any one bush, this can be done quickly and accurately. Preliminary trials were made to make sure that collections from the same set of bushes on different days produced essentially similar ratings.

Length of longest tertiary.—

From representative inflorescences, selected as described in the previous section, a representative secondary branch was selected as follows: On many plants all the secondary branches were closely similar; on some plants the terminal or the basal secondaries might be differentiated; on a very few plants there was a good deal of variation in the size and shape of the secondaries in any one inflorescence. A secondary branch was chosen from the mid-portion of the inflorescence for which

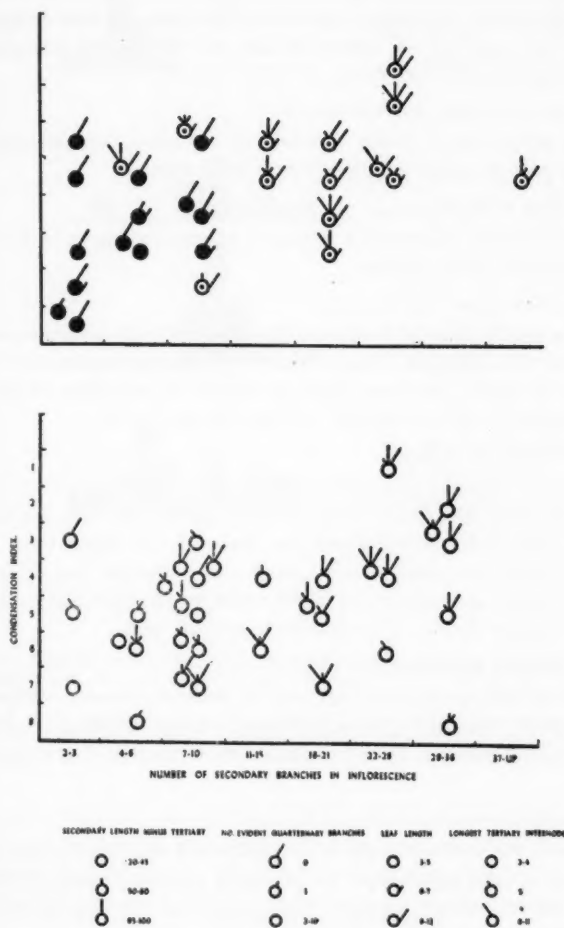


Fig. 5. Pictorialized scatter diagrams showing two collections of *Adenostoma* from Palo Alto. Below, random sample plus 1 or 2 selected extremes. Above, collection of every plant from a dry summit (solid black) and a collection of an equal number of plants from damper slopes among oak trees. In both diagrams the horizontal scale represents the number of secondary branches in the inflorescences. The vertical scale shows a condensation index from 1 (open) to 8 (very dense). This index combines two measures of density by adding the number of flowers per node to the number of condensed nodes out of five successive nodes.

there were several other secondaries matching it in size and shape (when, as in the dense extremes there were only one or two secondaries, then the least damaged one was chosen). The length of the longest tertiary on this selected secondary was measured with calipers and a steel ruler.

Length of the secondary inflorescence.—

A secondary inflorescence, chosen as previously described, was measured with calipers from its junction with the primary stem to its apex.

Longest tertiary internode.—

On the longest tertiary inflorescence previously chosen, the length of the longest internode was measured with calipers.

Number of flowers per node.—

The characteristic number of flowers at either side of each apparent node was recorded. Due to telescoping of successive nodes an apparent node might be two successive nodes, in which case there would be flowers on both sides of the stem. The number scored was that on one side. It varied from 1 to 3.

Number of condensed nodes.—

A tertiary branch chosen as described above was examined carefully at its base. Five successive apparent nodes were scored, and the number of these five nodes at which adjacent nodes had been telescoped was recorded. It varied from "0" in some plants (in which case there were no condensed internodes and the tertiary branch bore its flowers alternately) to "5" in which case condensation at each apparent node produced flowers borne oppositely at each node.

Number of evident quaternaries.—

Many of the selected tertiary branches bore no evident quaternary branches at the lowermost nodes. Among the dense extremes, however, quaternary branching was sometimes highly developed, and a few plants bore as many as 6 or 8 quaternary branchlets.

Leaf length.—

After the work was well advanced it was discovered that leaf length, though relatively uniform in some populations, varied widely and significantly throughout the species. It was accordingly measured with calipers by selecting typical leaves from each specimen.

Parenthetically, it may be worth noting that the chief variables in these inflorescences are surprisingly similar to some of those which differentiate the inflorescences of various races of maize. Condensation (the telescoping of successive nodes) was first described by me in *Zea Mays* (Anderson, 1944). I thought of it at the time as a phenomenon peculiar to cultivated cereals, a teratological abnormality which man had put to good use economically. Not till much later did I gradually come to realize that it is a widespread phenomenon among wild and cultivated species in various families of the flowering plants. I have detected it in *Dactylis*, *Cichorium*, and *Pbiox*, in every instance as one of the results of hybridiza-

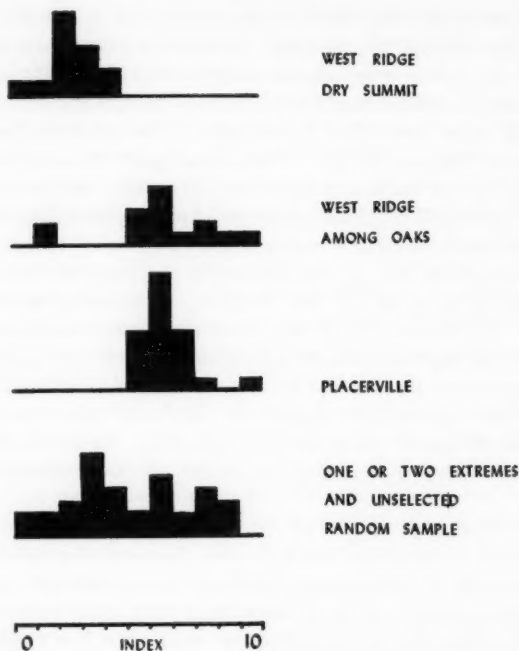


Fig. 6. The collections of fig. 5 plus an additional collection from Placerville ("mother lode"), diagrammed as frequencies on a hybrid index which runs from 0 for the low dense extreme to 10 for the tall open extreme. The index is formed by combining the five characters (the two characters used on the horizontal and vertical axes plus the three characters used on the rays), giving equal weight to each: lowest third, 0; middle third, 1; upper third, 2. A plant scored as 10, for instance, was in the upper third of the scale for each of the five characters.

tion between well-differentiated taxa. It is a phenomenon worthy of investigation by some one thoroughly conversant with the literature and concepts of plant morphology.

POPULATION STUDIES

As soon as the fundamental variables at the base of most of the variation in *Adenostoma* inflorescences had been apprehended, a large population was collected and analyzed. This was selected slightly west of Stanford University, at one of the localities where W. S. Cooper made his classical studies of the chaparral over thirty years earlier. Here the chaparral clothes many acres of rolling upland, the general appearance being surprisingly close to that of a British moorland. *Adenostoma fasciculatum* was the commonest species in this association and in some areas composed virtually all the shrubby vegetation.

An attempt was made to make as random a selection as possible. Surveyor's lines had been cut through the chaparral. These were followed on foot, and inflorescences, one to a plant, were selected roughly every ten or fifteen feet. Care was taken to select an inflorescence from a vigorous branch and one that was representative of the plant from which it was taken. The results are presented as a pictorialized scatter diagram in fig. 5. Those desiring an elementary exposition of this graphical device will find one in Anderson, 1952, with a minimum of technical phraseology. A technical discussion of the basic philosophy underlying the technique has recently been published (Anderson, 1954).

From fig. 5 it is clear that all the measurable plant-to-plant variation in this population sample is in two closely knit complexes with various intermediates and recombinations. At the one extreme is a small dense inflorescence, the individual flowers so closely set together as to be indistinguishable without careful examination. The inflorescences are tiny but may be scattered in large numbers over the surface of the bush. At the other extreme are big plummy inflorescences something like open panicles of lilacs. They are held high above the bushes on wand-like branches and are so open that the individual flowers are clearly recognizable as such at first glance.

By the method of extrapolated correlates (Anderson, 1949) it is possible to draw up precise technical descriptions of the taxa responsible for such introgressive complexes as this one in *Adenostoma*. Without further information one would have no means of knowing whether he was looking for a taxon more extreme than the "large open", or one more extreme than the "small dense", or perhaps for both. At just this point in the investigation Dr. G. Ledyard Stebbins (who had been following the investigation with much interest) brought me a population sample from the "mother lode" country at the base of the mountains on the east side of the great central valley of California. This proved to be made up exclusively of the large open-panicled extremes, the general average of the entire collection made by Stebbins, being about equal to the most extreme plants in the random collection from Palo Alto. The simplest hypothesis (since this taxon was apparently in existence in another part of California) was that the *Adenostoma* of the coastal chaparral, the *Adenostoma* we had been studying, represented extensive introgression of the same open-panicled sort by a low dense kind even more extreme than the lowest and densest which had turned up in the random sample. I then drew up a description of this hypothetical extreme, character by character, adding a few more characters from the examination of the lowest-densest extremes from the random collection. Theoretically, we should hope to find a low bush *Adenostoma*, with short leaves, with expanded blades, not so needle-like as those we had been studying. It should have extremely dense inflorescences, borne as single panicles of the current season's growth, the entire inflorescence no larger than the end of a man's thumb. The hypanthium (the lower surface of the bloom) should be pubescent. This description was then run down in Jepson's *Flora*, just as though we had the specimen at hand. It led to *Adenostoma fasciculatum* var. *obtusifolium*. Jepson's description answered our extrapolation in all respects except that it made

no mention of pubescence. Examination of typical specimens of var. *obtusifolium* in the Dudley Herbarium at Stanford University showed that just such a pubescence was indeed found in this variety.

Adenostoma fasciculatum var. *obtusifolium* is a characteristic plant of the Channel Islands and a few rocky headlands along the southern coast of California. According to our interpretation, the highly variable *Adenostomas* of the coastal chaparral resulted from extensive introgression of a tall plummy *Adenostoma*, similar to those now growing in the oak savannahs of the "mother lode" country, with this low shrub from foggy headlands along the coast. Each of these had its own contribution to make to life in coastal California. The latter was accustomed to growing in shallow, rocky soil, under intense radiation, with virtually no shade, but with abundant rain and frequent fog and drizzle. The former was accustomed to deep soil and partial shade, but it was bred to dry air, extensive seasons of extreme drought, and to baking heat.

With this new understanding I returned to the locality in which the original collection had been made. The basic ecology of the site almost fell into place at once, when interpreted in the light of this analysis of variation in *Adenostoma*. The low extremes were growing on rocky, thin-soil summits or on little ridges. The big plummy ones were on north slopes, particularly in those spots where there was water seepage in the early spring. The strangest of the bizarre recombinations were to be found in the semi-abandoned corral back of an old ranch, where man and his animals had made strange new ecological niches in the edge of the chaparral. Two collections were made from two extreme habitats and are shown in figs. 5 and 6. For the first collection every plant was sampled on a rocky little ridge; the second was made from moist spots in the shade of oaks at the northern edge of the chaparral, both sites being within the area where the original random collection was made. It will be seen that the populations of these two extreme habitats are outside the range of variation of each other and that the tall plummy extremes are fairly equivalent, on the whole, to Dr. Stebbins' collection from the "mother lode" country, at Placerville.

By the time these collections were analyzed, my term as a Visiting Stanford Professor had come to a close, and it was not possible to make further field studies of these plants. There remains to point out the bearing of this technical analysis on the general problem of the chaparral and its origin.

It is known from paleontological evidence that habitats similar to the oak savannah of the "mother lode" country and the coastal headlands of southern California had a history going back at least into the Tertiary. Chaparral vegetation is relatively new. There are those, like Carl Sauer, who view it as largely post-human; an ecological artifact brought about by large scale burning. There are others who admit that it has been strongly influenced by man but believe the chaparral, though relatively recent, to be definitely pre-human. The studies reported above do not settle this argument but they do present a new set of techniques by which significant data can be gathered for solving such problems.

As my field studies of *Adenostoma* drew to a close, I came to realize that the chaparral, as a whole, is made up not only of introgressive complexes of *Adenostoma* but of other genera as well. Of all the samples of the world's vegetations with which I have had personal experience it is, as a whole, the most wildly variable collection of intergrading complexes. It is variable, plastic, and at the present moment is vigorously differentiating into new types and sub-types under the impact of man, "an ecological dominant" (Sauer, 1952). To the student of evolution it presents an enormous outdoors experimental plot in which one can study not only the catalyzing effect of man upon the chaparral; it is a laboratory in which can be investigated the special problems of *all* such floras thrown into flux, of rapid evolutionary change as the result not merely of man but of any ecological dominant. The evolutionary problems of the California chaparral are essentially similar to those of the first land plants, to the evolution of floras under the impact of the first great herbivores, to the special problems of any of those times of rapid catastrophic impingement of one set of organisms upon another (Anderson and Stebbins, 1954).

The studies reported here were carried out in May and June of 1952 when I was Visiting Professor of Biology at Stanford University. I am greatly indebted to Dr. Twitty and various members of the departments for many courtesies and to Dr. Richard Holm and the staff of the Dudley Herbarium for technical help, tactful forbearance, and stimulating companionship.

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